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Multispecies Approaches to Fisheries Management Advice

M. C. Mercer

Canada

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MULTISPECIES APPROACHES TO FISHERIES MANAGEMENT ADVICE

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M. C. MERCER [ED.]

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DEPARTMENT OF FISHERIES AND OCEANS
Ottawa 1982

Frontispiece: "Big fish eat little fish" by Pieter Brueghel d.Ä. 1556, pen in grey ink; H 216 mm, W 302 mm. Courtesy Graphische Sammlung Albertina, Vienna, Austria.

Dedication

The year 1981 marked the 50th anniversary of fisheries research in Newfoundland, dating from the establishment of the original Fisheries Research Institute at Bay Bulls, near St. John's. This Special Publication constitutes the proceedings of a workshop convened in the new Northwest Atlantic Fisheries Centre in St. John's and is dedicated to the substantial contributions made by fisheries researchers in Newfoundland over the past half century.

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Abstract

MERCER, M. C. [ed.] 1982. Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59: 169 p.

This Special Publication comprises the proceedings of an international workshop convened at the Northwest Atlantic Fisheries Centre in St. John's, Newfoundland, November 26–29, 1979. The purpose of the workshop was to discuss the results of recent multispecies research, its applications to management, and to consider future directions for research in this field. A total of 26 papers were presented, including a combination of experience papers, state-of-the-art review, and new scientific findings. Sequential sessions were held on fisheries systems research by Canada Department of Fisheries and Oceans, multispecies considerations in fisheries research and management advice in the ICES area, species interactions in the Northeast Pacific and Northwest Atlantic, fisheries interactions, and applications to fisheries management. The workshop concluded with a substantial discussion of implications of present knowledge for advice to fisheries managers and implications for research program planning. The Workshop Report comprises the Chairman's opening remarks, a report on main elements of discussions in the sessions, and a summarization of workshop conclusions.

Key words: multispecies, ecosystem management, fisheries management strategies, fisheries, management, fisheries models, predation, modeling

Résumé

MERCER, M. C. [ed.] 1982. Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59: 169 p.

La présente publication est un compte rendu d'un atelier de travail international convoqué au Centre des pêches de l'Atlantique nord-ouest à St-Jean (Terre-Neuve) du 26 au 29 novembre 1979. Le but de cette réunion était de discuter les résultats des récentes recherches multispécifiques et leurs applications à la gestion, et d'examiner l'orientation future de la recherche dans ce domaine. Un total de 26 communications y ont été présentées. Elles traitaient, entre autres, de résultats d'expériences, d'une revue de l'état de nos connaissances et de récentes découvertes scientifiques. Des séances successives furent consacrées à la recherche menée par le ministère des Pêches et des Océans du Canada sur les systèmes halieutiques, à l'aspect multispécifique de la recherche sur les pêches et des conseils de gestion dans la zone du CIEM, aux interactions entre espèces dans le Pacifique nord-est et l'Atlantique nord-ouest, aux interactions entre pêcheries et implications pour la gestion. L'atelier de travail s'est terminé par une discussion en profondeur des applications de nos connaissances actuelles aux conseils offerts aux gestionnaires et à la planification des programmes de recherche. Le rapport de l'atelier de travail comprend les remarques d'ouverture du président, les principaux éléments des discussions et un résumé des conclusions.

Preface

In recent years literature in the field of renewable resource management has shown increasing emphasis on the concept of ecosystem or multispecies approaches. The concept of moving resource management strategies in this direction has found support in a range of circles including the resource harvesters, other interest groups, and governmental policy-makers. The subject will not be explored further in this preface as the introduction to the Workshop Report provides additional background. There are thus significant implications in theory both for resource management and for the scientific programs required to support such management. Accordingly, the Canada Department of Fisheries and Oceans decided in 1978 that it would be useful to convene a workshop to discuss the results of recent research, its applications to management, and directions for future research in this field.

A Steering Committee to undertake organizational work was convened under my chairmanship and included E. J. Sandeman, J. S. Campbell, R. Beamish, and W. G. Doubleday, to whom I am indebted for their efforts. The workshop was held at the Northwest Atlantic Fisheries Centre, St. John's, Newfoundland, November 26–29, 1979, with 49 participants present. The participants were drawn from research organizations in Canada, the United States, and Western Europe, with the intent that the workshop focus on research experience in the North Atlantic and Northeastern Pacific. Approximately one-third were drawn from outside the Government of Canada and approximately two-thirds were present by personal invitation, the remainder being selected by the directors of Canadian fisheries laboratories.

The workshop was organized into six separate sessions, each with its individual chairman and rapporteur (see Workshop Report). Papers presented in each session were discussed individually, followed by a general discussion of the subject matter of the session. Chairmen and rapporteurs then produced session reports which were subsequently revised and their substance was incorporated by me in the Workshop Report which constitutes part of this volume.

A total of 26 papers were presented, all but a few of which were specifically invited to cover carefully selected subject areas. Accordingly, the mix includes a combination of experience papers, state-of-the-art review, clearly new scientific findings, and analyses containing primarily negative results. Following the workshop each paper was reviewed by the relevant session chairman and received outside review by at least one and generally two other referees prior to final editing for inclusion in the volume.

I would like to thank all who participated and contributed to making the workshop a success, with special thanks to session chairmen, rapporteurs, and the many referees who cooperated in facilitating final completion of the papers for publication. I would like to express particular appreciation to Mr E. J. Sandeman, then Research Director at the Northwest Atlantic Fisheries Centre, and his staff for the excellent facilities and arrangements provided for the meeting.

M. C. Mercer
Convenor, Chairman,
and Special Editor

Multispecies Approaches to Fisheries Management Advice: Workshop Report

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Introduction to the Workshop

WORKSHOP CHAIRMAN: M. C. MERCER

A policy paper issued by the Government of Canada (Anon. 1976) rejected maximum sustainable yield as a guiding principle in fisheries management in favor of "best use of society's resources." The paper set a policy course of fisheries management on an ecosystem basis in line with current thinking in resource management.

In fiscal year 1978 the Canada Department of Fisheries and Oceans spent more than $37 million on fish stock assessment and related research. It is thus a matter of some consequence whether such resources are most effectively deployed in relation to policy objectives. Although there is general recognition of the importance of multispecies considerations in the dynamics of exploited fish stocks and the viability of commercial fisheries, there has been no formal evaluation and planning of multispecies related research and guidelines for management advice to date in Canada. It was thus felt appropriate to convene this workshop to discuss the results of recent research, its application to management, and directions for future research.

The subject area is not one that has escaped previous recognition. Indeed a colloquium on the multispecies problem was held in June 1976 under the sponsorship of the United States National Marine Fisheries Service (Hobson and Lenarz 1977). More recently an expert consultation on multispecies problems was held under the auspices of the U.N. Food and Agriculture Organization in September 1977 (Anon. 1978). There is thus considerable background on which we can draw during the present workshop and several of the participants in the present workshop were participants in the two meetings to which I have just referred.

SINGLE SPECIES MANAGEMENT

Traditional approaches to fisheries management, both in terms of stock assessments and management policy, have tended to treat species as if they existed independently of other species and were harvested independently of other species. This approach ignored the technological interactions, whereby capture of one species also resulted in capture of other species, and the biological interactions involving predation and competition. The inadequacy of this approach has become of increasing consequence over the past 2 decades with the tremendous expansion in the intensity of fishing operations and an increase in the variety and trophic levels of species harvested.

MAXIMUM SUSTAINABLE YIELD

A concept which has deep roots in the fisheries literature and which has suffered its toll of attack in recent years is that of maximum sustainable yield (MSY), i.e. the maximum harvest that can be taken in perpetuity from a self-regenerating stock of animals. The recent literature abounds in critiques of MSY both in terms of conceptual difficulties of a biological nature and application of the concept as a management objective (e.g. see Holt and Talbot 1978; Sissenwine 1978; May et al. 1979). I will not belabor the arguments here; indeed, as an epitaph of the concept has already been published (Larkin 1977), I could be accused of resurrecting a dead horse for purposes of flogging it.

ALTERNATIVE APPROACHES

Although MSY was often embraced as a management objective by virtue of being the lowest common denominator in terms of the disparate social and economic interests of states competing for common property resources, the advent of extended fisheries jurisdiction has at least offered a greater possibility for stocks to be managed on the basis of some other "optimum." It is thus of interest to look at alternative management objectives that have emerged.

One of these is the concept of optimum sustainable yield (OSY) as generated by an American Fisheries Society symposium on the topic (Roedel 1975). There OSY was defined as "a deliberate melding of biological, economic, social, and political values designed to produce the maximum benefit to society from stocks that are sought for human use, taking into account the effect of harvesting on dependent or associated species." This concept, which embraces multispecies considerations among others, is not readily transposed into the operational context of management decision-making.

One of the single species approaches to "optimum yield" which has had recent wide application in management of Northwest Atlantic groundfish has been to aim for a target fishing mortality of $F_{0.1}$, i.e. the level of fishing mortality for which the marginal increase in yield per recruit due to a small increase in F is 1/10th of the marginal increase in yield at very low levels of F. Depending upon the shape of the yield curve this strategy may allow the taking of 80–90% of the catch at F_{max} but with approximately two-thirds of the effort. While this target has both biological and economic advantages, the $F_{0.1}$ level does not possess unique merit that could not be replaced, particularly if given hard socioeconomic data as a basis for selection of a management strategy.

Another interesting concept emerged with the passage of the United States Marine Mammal Protection Act of 1972 (16 USC 1351-407) which expressed an American policy that "species and population stocks of marine mammals should not be permitted to diminish below their optimum

[1]Workshop Chairman.

sustainable population (OSP)." Although the Act dated from 1972, the definition of OSP was not published until December 21, 1976 (41 FR 55536) as "a population size which falls within a range of the population level of a given species or stock which is the largest supportable within the ecosystem to the population numbers or biomass resulting from additions to the population due to reproduction and growth less losses due to natural mortality."

We may note also recent efforts by conservation organizations to develop management principles replacing MSY. For example, the International Union for the Conservation of Nature and Natural Resources (IUCN) suggested certain principles in Resolution No. 8 of its 12th General Assembly. The principles included the following:

1) The ecosystem should be maintained in such a state that both consumptive and nonconsumptive values can be realized on a continuing basis, ensuring present and future options, minimizing the risk of irreversible change or long-term adverse effects.

2) Management decisions should include a safety factor to allow for limitations of knowledge and imperfections of management.

3) Measures to conserve one resource should not be wasteful of another.

4) Survey or monitoring, analysis, and assessment should precede planned use and accompany actual use of a resource and the results should be made available promptly for critical public review.

These principles emerged from two workshops convened in 1974–75 (Holt and Talbot 1978).

Multispecies Management

It is apparent that the limitations of single species approaches to fisheries management are recognized and the pitfalls of adopting maximum sustainable yield as a management objective well elaborated. The multi- cies or ecosystem approach to resource assessment and development of management advice is accepted in principle as is the idea of managing a resource to achieve social and economic benefits, not simply a readily calculable physical yield.

Workshop Organization and Outputs

Given the foregoing, it is appropriate to review priorities in our research programing in the field of resource assessment. Should we continue to direct most of our studies to the biology and population dynamics of single species? Should we be increasing research towards understanding production at lower trophic levels? Should there be an intensification of studies of predator/prey and competitive relationships? Do we know enough today or are we likely to learn enough in a short time horizon to make quantitative predictions on the effects of harvest of any species on the yields of its competitors, predators, or prey? How do we tackle the problem of harvesting forage fish when their predators support important commercial fisheries?

These are some of the questions that I hope we will be able to consider over the next 3 d. In this regard I would like to make a few comments on the organization of our workshop and its intended outputs.

The opening day is structured to provide a general overview of progress in the field of multispecies approaches to fisheries management with particular reference to work that has been conducted in the North Atlantic. The morning session is devoted to research conducted at the Marine Ecology Laboratory, Dartmouth, Nova Scotia, which was established 10 yr ago as a fisheries "futures laboratory" by the late Fisheries Research Board of Canada in order to address long-term fisheries research problems. The afternoon session will review the current status of studies in the Northeast Atlantic where much of the focus of debate has been in the International Council for the Exploration of the Sea (ICES).

On day 2, the morning session will focus on species interactions with particular reference to recent research in two areas of particular interest to Canada, i.e. the Northeast Pacific and the Northwest Atlantic. In the afternoon we proceed then from the biological to the technological when we consider the subject of fisheries interactions, including a review of the question of species succession.

Day 3 begins with a session on applications of multispecies considerations to fisheries management wherein we will review the impact of advice, based on multispecies considerations, on management measures adopted, and the effects of these management measures. Then in the afternoon we will begin consideration of the implications of our deliberations for advice to resource managers today and implications for research program planning. The intent is for us to break into four syndicates to prepare independent reports on these two key issues. The reports will be brought forward for discussion at our wrap-up session on the final morning.

Before closing, I stress again the focus of our discussions on the biological–technological considerations of multispecies problems in the fisheries system. We have purposefully not ranged deeply into areas of environmental trends or stochasticity or into the emerging field of bioeconomics. To do so would force our workshop to become a much more unwieldy, if more comprehensive, exercise.

The outputs of the workshop are intended to include the following: (1) provision of advice to research and fishery managers which will be of value in planning resource assessment research and generating management advice, taking into account multispecies considerations, and (2) a special publication of multispecies approaches to fisheries management which will include the papers considered at this Workshop and the Rapporteurs' Reports on each of the sessions. This is to be published by the Department of Fisheries and Oceans.

Fisheries Systems Research by Canada Department of Fisheries and Oceans

Chairman: S. R. Kerr Rapporteur: E. J. Sandeman

The Marine Ecology Laboratory (MEL), a component of the Bedford Institute of Oceanography, has since its establishment been a contributor to the development of multispecies approaches to fisheries management in Canada. Accordingly, this session was given over to a general survey of the MEL experience and the papers presented address general aspects of that experience.

First, a brief account of the genesis and development of the MEL indicates how the ideas that characterize the MEL approach came to be formed and developed. The next two papers examine the MEL approach in more detail, the first of these in terms of the implications of multispecies analysis for management science, the second in terms of the apposite modeling approach to complex systems. The final two papers of the session then survey some results of the application of the MEL approach, one in the general context of prediction for multispecies fisheries, the other by considering interactions between the mammal and fish components of marine production systems.

1) L. M. DICKIE AND S. R. KERR: *Alternative approaches to multispecies management*

In discussion, concern was expressed that a most important general point had been omitted because the authors had ignored the way in which commerce operates and because the behavior of fishermen is so often directed by companies which in turn are responding to market demands and the provision of goods to these markets. External trading may thus often affect local demands on the fisheries resources of a region. In response it was suggested that this point was contained within the concept of a self-regulating industry for which examples were said to be few.

The problem of statistical data requirements was addressed at length. This is a complex question and statistical systems tend to be massive as well as requiring long time series of data. In part, the solution to this problem appears to lie in more appropriate scaling of data-gathering to the fishery being monitored. In this respect it is important to distinguish between research needs which are generally small and management needs which tend to be massive.

It was suggested that single species stock assessment models are doomed to failure because the underlying "particles" are not well behaved.The reply was that by "external" methods of analysis of integral systems we should be able to determine appropriate well-behaved variables for observation.

2) W. SILVERT: *Top-down modeling of multispecies fisheries*

Discussion of this paper centered around the basic philosophy of modeling, and the importance of preconceptions in the approaches. Although some confusion obviously existed in defining "top-down" as opposed to "bottom-up" modeling techniques and their application to the problem at hand, at least one modeler present expressed the opinion that the "top-down modeling of multispecies fisheries was the only way to go."

3) R. W. SHELDON, W. H. SUTCLIFFE JR., AND K. DRINKWATER: *Fish production in multispecies fisheries*

Most discussion related to the extrapolation of primary production estimates to derive estimates of fish production and standing stock. Some questioned the technique on the grounds that it is open to the inherent dangers of extrapolation, an argument elaborated further in general discussion below.

4) P. F. BRODIE AND A. J. PÅSCHE: *Density-dependent condition and energetics of marine mammal populations in multispecies fisheries management*

In response to a question concerning field information on condition and stock density in marine mammal populations, discussion centered on blubber thickness as an indicator of condition, as well as on behavioral aspects such as increased fighting among mature male seals in situations of relatively high stock density. Obtaining satisfactory estimates of daily food requirements remains a difficult problem, with aquarium-derived estimates appearing high relative to the wild where behavior is substantially different.

The general discussion of the session focused on several elements.

a) System identification. A commentator made the following points concerning the Southern Ocean. It is clear that all biological systems are complex and that some are more complex than others. It is also true that apparent complexity is a function of our relative ignorance. The question can then be raised as to how much the perceived complexity is a function of this ignorance. In the case of the Southern Ocean it seems the system might be simpler in terms of interacting elements (perhaps also a function of our ignorance). Also, the approach to modeling in the context of this area is determined not only by our perceptions of the biological system but also by the nature of the management systems that are emerging. Thus the biological models are being developed as integrations of single species models in this area. Furthermore, attempts at generalization may be dangerous if these take place without reference to area. To a large extent it is the reality of the political structures that leads to the "curious anachronism" referred to by Dickie and Kerr's paper. Aggregation of single species may not be too unreasonable in the context of the Southern Ocean.

In response, it was noted that system complexity is a function of the potential richness of human interaction with the system. If we can interact with the system in a variety of ways, i.e. measure many variables, it appears complex. We should not be intimidated by complexity nor should we be preoccupied with it. We should approach complexity by examining the integral behavior of the system and thereby derive the variables that can most usefully be applied for management. The complexity of a model is a function of the information that must be processed and the outputs required. In general, the amount of information is determined by both the number of variables being considered and the precision required.

b) Based on MEL experience, what is achievable in the next few years in relation to predicting production of commercial fish stocks? In response to this question it was suggested that although a detailed answer was difficult some useful tools were now available, particularly for general prediction (e.g. Sheldon et al. this workshop). However, not enough serious effort has yet been devoted to looking at fisheries as whole systems. The middle future, as opposed to the short-term future, appears the most promising, and then only if research is channeled in that direction. In the

shorter time frame, Sutcliffe's (1972) environmental correlations have provided useful predictions with respect to several stocks in the Northwest Atlantic. The particle-size distribution hypothesis of Sheldon et al. (1972) has scarcely begun to be exploited.

c) The difficulty of incorporating socioeconomic parameters in models was addressed briefly. Socioeconomic factors are important in regulating fisheries systems but they operate on different time scales and are subject to exogenous variations. The need to take advantage of natural controls and self-regulating aspects of the system was noted, as well as the need to develop methods of quantifying socioeconomic factors.

d) In response to a question about the costs of managing fisheries and possible cost–benefit implications of obtaining better understanding, it was suggested that this was a major incentive for adopting the multispecies approach with both simpler models and simpler management schemes, which can take advantage of the self-regulating features of the system. Reference was also made to a paper on the "price of knowledge" or risk in fisheries versus the cost of research (Silvert 1978).

e) St. Margaret's Bay. In response to a question as to whether or not we can now predict the fisheries production of St. Margaret's Bay, a major study area, the response was that this bay was not chosen for such prediction. The main thrust of its study was toward developing an understanding of the processes of energy transfer and their efficiencies. In general, the scientific results had met these broad aims with the added bonus of providing a training ground for developing interdisciplinary research programs. Commercial fish production in St. Margaret's Bay is trivial and its prediction was not a program consideration for that reason.

f) Experimental management. Although there are instances of experimental management of specific single species fisheries (e.g. Pacific halibut (*Hippoglossus stenolepus*) and fur seals), no such attempts appear to have been made in the multispecies context. It was noted that some of the tropical species complexes (e.g. in the Gulf of Thailand) may be prime candidates for planned experiments involving increased mesh sizes. It was noted that many changes in fisheries regulation could be regarded as experimental in nature although they usually lacked well-defined objectives, suffered from external uncontrolled effects, and lacked adequate evaluation. Where a deliberate attempt was made at experimental management of tropical tuna, the use of a fallacious model, which failed to anticipate that the fishermen would adapt to the management actions, doomed the experiment to failure.

g) Society's complex objectives. The ability of simple models to cope with the complex objectives of society was addressed from several different viewpoints. The necessity of demonstrating the real costs of achieving fisheries management objectives was noted, and many of the complexities were reviewed, e.g. multinational fisheries, marketing requirements of different species and sizes of fish, political or economic stability, and other such considerations.

Multispecies Considerations in Fisheries Research and Management Advice in the ICES Area

CHAIRMAN: S. J. HOLT RAPPORTEUR: J. G. POPE

The session was intended to review the current status of multispecies modeling efforts in the Northeast Atlantic where an ICES working group had recently been established to address the issue. Three papers were considered.

1) E. URSIN: *Multispecies fish stock and yield assessment in ICES*

Discussion of the presentation was largely concerned with the detailed structure of the Danish multispecies model, with emphasis on the predators' preference matrix and the ration size of predators. The author observed that the model faces two kinds of complaints: (a) that it is too complicated and (b) that it contains insufficient detail.

2) R. JONES: *Species interactions in the North Sea*

Discussion of this paper centered on three main points: (a) the estimates of primary production and food web efficiency used by the author, (b) the problems of replacement in complex systems and of the consequent problems of prediction, and (c) what advice should be given to fisheries managers. The author indicated his preference for providing advice regarding effort rather than yield.

3) J. G. POPE AND B. J. KNIGHTS: *Simple models of predation in multi-age multispecies fisheries for considering the estimation of fishing mortality and its effects*

In discussion, questions about details of feeding rates and their dependence on prey abundances were raised as was the question of whether the models could be used for predictions. It was argued that a nonpredictive model is not very useful and the aim should be to set up testable hypotheses. Johnson quoted Scriven (1959) to the effect that in the physical sciences if you can explain you can predict but in irregular subjects such as biology even if you can explain you can't necessarily predict. Pope suggested that some prediction might be possible in terms of the right direction in which to change fisheries even if precise values of F_{max} could not be computed. The point was also made that models can at least catalog our knowledge of the system.

Discussion then addressed the extent to which models helped define data requirements. Several points were made. (a) The need for annual stomach content budgets for important predators including the need to identify the life stages of prey and their positions in the trophic web. In particular it was suggested that energy flow in the benthos is poorly understood. The budgets could be used to set up and later to test multispecies models such as the cohort models or the Danish model. (b) Study of spatial distributions and seasonal and annual variations in overlap in prey and predator and the desirability to monitor routinely as much of the marine system as possible so that changes in abundance may be recognized as they occur. Although this has significant resource implications, it was suggested that much of the relevant monitoring is currently being done although sometimes not well enough.

Species Interactions

CHAIRMAN: B. E. BROWN RAPPORTEUR: J. S. CAMPBELL

Six papers were presented at this session, the first two concerning the resources of the North Pacific, and the others,

those of the Northwest Atlantic. Because many common themes and issues emerged in discussion, the papers are listed and discussion points are consolidated in a single section following.

1) T. LAEVASTU, F. FAVORITE, AND H. A. LARKINS: *Resource assessment and evaluation of the dynamics of the fishery resources in the Northeast Pacific with numerical ecosystem models*

2) F. FAVORITE AND T. LAEVASTU: *Ocean migrations of salmon and estimation of carrying capacity of the North Pacific Ocean*

3) M. P. SISSENWINE, B. E. BROWN, J. E. PALMER, R. J. ESSIG, AND W. SMITH: *Empirical examination of population interactions of fishery resources off the northeastern United States*

4) E. B. COHEN, M. D. GROSSLEIN, M. P. SISSENWINE, AND F. STEIMLE: *Energy budget of Georges Bank*

The last two papers dealt with the area off Nova Scotia.

5) J. D. PRINGLE, G. J. SHARP, AND J. F. CADDY: *Review of the interaction between carnivores, herbivores, and benthic macroalgae in the Northwest Atlantic and the implications on fishery management*

6) T. AMARATUNGA: *Impact of predation by Illex illecebrosus on the Scotian Shelf*

Discussion related primarily to three major issues.

a) Model selection and parameter inputs. Considerable discussion by the participants concerning the use of empirical models indicated that if one accepted an empirical model, one could estimate the parameters of the model indirectly, but that difficulties would then occur in estimating the interaction term. A speaker questioned the value of fitting parameters empirically to such a model which theoretically ill describes the functional response. It was noted that models serve as data filters and that parameter estimates summarize whatever signal is available from the data and that it is thus important to select models with a minimum number of parameters; otherwise some of the noise may be incorrectly interpreted as signal. It was also noted that although it may appear that a more detailed model is a closer approximation to reality, this could be a fallacy and a simpler model may be more robust and thus more appropriate for describing the overall system. It was also observed that if marine ecosystems are not stable then the models themselves need not be stable. The importance of selecting models that include both environmental factors and biological interactions was noted and it was argued that models that include environmental factors directly rather than as noise may be preferable. The importance of sensitivity analysis was discussed with particular reference to shifts in fish diet in models of feeding interactions as well as changes in consumption rates in key predators such as marine mammals. The energy budget discussions concentrated on the question of potential energy sinks and whether a large share of the benthic productivity on Georges Bank might reside in the large benthic molluscan complex. It was also noted that the tremendous abundance of echinoderms on Georges Bank might also be a factor in this energy sink. The parameters used for production/biomass for squid were questioned as possibly being too low and it was noted that the finfish production/biomass ratios would be somewhat higher if 0-group fish had been used in the calculations. Further, these changes might make the difference between the Georges Bank and North Sea models and lessen the contrasting comparisons between primary productivity and finfish productivity.

b) Stability versus instability in systems. Discussions explored the usefulness of making steady-state approximations in model development to understand a system, as the instability in a system is most difficult to interpret. The difference between simulation and parameter estimation was noted and it was pointed out that when the environment is not constant, then the values of parameters that are estimated may be fallacious when used in a predictive mode. Discussions suggested that the question of whether, in general, a model should be stable or unstable is irrelevant; more appropriately a model must conform to the natural process being modeled with the understanding of the underlying process translated into mathematics. It was stressed that estimators of parameters are themselves modeled and that modelers of marine systems are always faced with the difficulty of obtaining precise enough estimates of biomass and year-class strengths. It was commented that in multispecies systems the greatest yield may actually come from a system that has been destabilized. In complex systems it is most difficult to find specific correlations simply by observing changes in the component system. If a component is a competitor, its changes in this case might "tip" the system toward another state. The recently observed increases in squid biomass in the Northwest Atlantic, as well as earlier in the Gulf of Thailand, both appeared to have followed a heavy finfish fishery.

c) Identification of environmental parameters. Discussions indicated that the driving force in many fish stocks is year-class strength which is affected by the environment. However, specific important environmental factors are difficult to identify. It was noted that there is a choice as to whether one applies an equilibrium type or transition state model; for the latter type to be useful the problem of environmental noise must be addressed. Mention was made of a model of flatfish production off the coast of Oregon where 85% of the variation in certain factors could be attributed to oceanographic parameters, specifically to aspects of upwelling. When the variance due to strong abiotic factors is filtered from background noise one can proceed more easily to investigate biotic factors. It was also suggested that it may be important to utilize statistical theory which would allow the explanation of unusual occurrences in fish stock abundance. It was generally agreed in many comments that environmental factors may be useful as covariants in models and might well be essential for longer term predictability in models.

Fisheries Interactions

CHAIRMAN: P. A. LARKIN RAPPORTEUR: M. D. GROSSLEIN

The management of multispecies fisheries embraces not only the situation in which one type of gear takes more than one species of fish at a time but in the broader and more realistic sense, it essentially means management of the fisheries of a region. The objective of such management is to achieve some desired pattern of harvesting of living marine

resources and it thus follows that there are many considerations involved.

In addition to the ecological interactions among the species of fish and the ecosystem of which they are a part, which involve both seasonal and spatial elements, there are considerations such as the behavior of fishermen, market factors, the tactics of fishing companies and the strategies of corporations, the impact of technological changes, and the realities of politics. The manager must not only obtain a great deal of information, but must develop suitable regulations and enforce them, reconciling the various participants in the fisheries to the inevitability of compromise, and working with the participants in the continuing need to set goals for the future.

One of the difficulties of such generally stated problems is how to conceptualize them in a form amenable to analysis. The three papers in this session give examples of some different approaches. The first, by Pope and Knights, compares size distributions which aggregate all the species taken in trawl surveys in the North Sea and at Faroe Bank. The second, by Healey, takes the five species of Pacific salmon and indicates the complications of managing the many stocks that are taken together in the fisheries, while acknowledging the social, economic, and political contexts. The third, by Paloheimo and Regier, deals directly with the problems of conceptualization, particularly as they bear on future management of the Great Lakes fisheries. As the discussion of these papers clearly shows, there are many more suggestions about what to include in what is to be treated as a system to study than suggestions for what to leave out.

1) J. POPE AND B. J. KNIGHTS: *Comparison of the length distribution of all demersally caught fish combined from surveys in the North Sea and at Faroe Bank*

In discussion it was noted that maintaining a population with more and older age-groups will provide more stable catches. It was suggested that mesh size in United Kingdom research vessel trawls would not sample sand lance adequately and further suggested that other explanations could be offered for the differences observed between the North Sea and Faroe Bank. One commentator noted the significance of a general problem of application of the definition of optimum yield in the United States. In mixed trawl fisheries it is very difficult to determine how to obtain optimum yield through application of minimum and maximum mesh sizes when accounting for all socioeconomic–political factors governing fisheries. It was suggested that this was probably less of a problem in the North Sea because fish of a wide range of sizes were marketable. It was argued that although individual species curves might show irregularities, one might expect a relatively smooth curve when all species size distributions are aggregated. It was further observed that concentrations of fishermen on aggregations of fish would probably tend to remove any bumps in the curve. If mesh size is shifted downward potential catch and the slope of the size spectrum curve would be increased. It was suggested that more uniform exploitation over the size range would be preferable to the current heavy exploitation of small sizes in the North Sea. It was noted that some recent unpublished work by Reed (subsequently published, Reed 1980) indicates that there are theoretical advantages for both minimum and maximum mesh sizes in dealing with species whose fecundity increases exponentially with age. The issue was raised whether the theoretical advantages referred to would actually apply in the case of a multispecies fishery with a broad spectrum of biological interactions. It was indicated that desired fishing strategies will vary with sizes, i.e. if the objective is large fish (truncate the curve) then employ large mesh and fish intensively, whereas if a wider size range is sought (i.e. slice the curve) then employ small mesh and fish less intensively. However, it was observed that if spatial segregation of sizes is not marked, then catch per unit effort would be substantially higher with a strategy of smaller mesh and lower fishing rate than with larger mesh and a higher fishing rate. It was argued that given sufficient knowledge of reproduction and predation patterns, it should be possible to calculate an optimum strategy for any given set of goals.

In final comment it was felt that it would be useful to examine pre-War biomass–length curves for the North Sea, and also for the pre- and post-heavy exploitation periods on Georges Bank; this might allow better understanding of the response of finfish biomass size structures to exploitation.

2) M. HEALEY: *Multispecies, multistock management problems in the management of Pacific salmon*

The availability of historical information on extermination of stocks was questioned in discussion. It was indicated that it was difficult to determine events prior to about 1950 because earlier data were mostly qualitative. Since 1950 there had been some runs lost as a result of environmental "catastrophes" but not apparently due to heavy fishing. It was noted that in the American salmon fisheries there were some additional problems. First, a greater proportion of the American fish are from hatchery runs and appropriate exploitation of these runs would eliminate native runs in the same stream system, whereas exploitation rates that are appropriate for the native fish would underharvest the hatchery runs. Second, the legislation mandating that Indians are entitled to the first half of a run greatly complicates the management problem because Indian fisheries are at the end of the "gauntlet."

It was suggested that in some ways, salmon fisheries managers may be in a better position than most to use multispecies models because they know the stock and recruitment values and can predict major variations in runs. For example, in the case of two stocks in British Columbia where temporal and spatial differences in runs were known one could use multispecies approaches to determine the method of fishing that would maximize benefits. However, it was stated that there may be hundreds of stocks in the same river system at the same time, and there is a need to protect the very small stocks. The question arose as to how one knows there are 3000 rather than far fewer separate stocks. The reply was that there is some "straying" but failure of natural runs to rejuvenate when wiped out by natural environmental events and strong homing behavior leads one to consider each run a unique genetic pool whose existence may be jeopardized by excessive fishing. It was added that wherever the stock identification question has been examined, a high degree of homing has been found, especially for sockeye (*Oncorhynchus nerka*).

Incidence of straying is considered to be relatively low but much of the evidence for straying is based on tagging which does not provide definitive quantitative measures.

In view of the wide scatter on stock–recruitment plots and the considerable difficulties encountered in the many attempts to identify environmental causes of variability, the question was raised whether Ricker's stock–recruitment (SR) curve concept was a valid approach for predicting recruitment and whether there are data to indicate that the observed large variability about the SR curves is caused by environmental variation.

It was suggested that the SR relationship works except in some special cases and is still a useful underlying regulator; some ongoing studies look very promising for explaining environmental causes of deviations from the SR curve, particularly the role of ocean currents. Although some felt there was no doubt that the SR relationship exists for salmon, they felt it is not very useful for predicting optimal yield or appropriate escapement especially in complex multispecies and multistock cases.

A question was raised concerning the possible benefits that might be achieved in terms of reducing complexity of management by moving the harvest further away from the spawning streams, i.e. fewer user groups and fewer "stocks" to worry about; this would pose substantial transition problems. It was further noted that shifting the harvest closer to the river mouths would simplify the problem but would be extremely difficult to implement in light of the pattern of user groups.

Some recent success was noted in relating coho (*O. kisutch*) and chum (*O. keta*) survival in the ocean to upwelling, and another ongoing study of Skeena River sockeye has revealed a strong correlation between smolt survival and oceanographic variables, notably upwelling, salinity, and amount of light. The most important variable was upwelling, which accounted for two-thirds of the variability observed in returns. Because the upwelling occurs some 9 mo before the spawning that will produce the affected brood, there is some possibility of capitalizing on this information in terms of management.

With three basic management objectives implied (i.e. (a) maintain high catches, (b) avoid allocation conflicts, and (c) prevent extermination of stocks), the question was posed that if one assumes some intermixing of stocks, why be concerned about extermination? The answer related to the political importance of each run, and an additional complexity in the United States relates to provisions of its Endangered Species Act.

3) J. E. Paloheimo and H. A. Regier: *Ecological approaches with multispecies resources in multiple-use situations in multistressed freshwater ecosystems*

Following this paper the session was opened to general discussion as well as comments on the Paloheimo–Regier paper. Remarks on the three foregoing papers are summarized here.

Discussion of the last paper focused on the relative importance of abiotic versus biotic factors, their implications for stability of multispecies systems, and the type of research needed to investigate the systems. One commentator suggested that if systems were controlled chiefly by biotic interactions then one could expect relative stability, but if abiotic factors exerted the principal control then the systems would be unstable. It was replied that both are known to be important and therefore in need of study with insight into the biological interactions being gained through modeling. It was suggested that although much variability in recruitment may be induced by abiotic factors there is still a considerable basis for management intervention. At least for the longer-lived species in multispecies systems it is possible to make reasonable predictions of the effects of heavy versus light exploitation levels.

One participant expressed concern that there are difficulties in developing predictive capability from environmental indices such as the correlations shown by Wickett (W. P. Wickett, Pacific Biological Station, Nanaimo, B.C., personal communication). Correlations with biological time series almost invariably collapse after a few years beyond the initial time series — they have a "half-life" of perhaps about 8 yr. Most correlations are related to sea surface temperature data for which the best time series are available, but linkage with many other physical properties which are undoubtedly operating may not be close. A respondent indicated that in this case one must identify which biological variables are responding to which abiotic factors. For example, one would expect to see rather direct temperature effects on ranges of migratory species but not necessarily on primary or secondary production or even total fish biomass. This raises the question of the likelihood of finding gross abiotic or biotic indices in multispecies systems on which to base a predictive capability. A warning was made not to overlook the possibility that correlations observed for specific periods of time may in fact represent real effects; their subsequent breakdown may result from appearance of additional factors. It is important to continue attempting to relate the biotic and abiotic events through careful sifting of available oceanographic and biological data within the framework of testing specific hypotheses based on knowledge of the life history of the species involved. Emphasis should be put on the larval and juvenile stages where the major factors controlling recruitment are operating. Another participant indicated that one should not be preoccupied with present inability to relate large recruitment fluctuations to abiotic factors; one can still apply purely biotic models to clarify multispecies system properties which can then be translated into useful advice for both short-term and long-term management strategies.

The possibility of experimental management approaches was noted, and it was observed that given current stock assessment techniques for long-lived species, it is not necessary to wait for long periods to measure effects of various management actions. However, it is necessary to deal with time lags imposed by effects of dominant year-classes. As the time series lengthen for frequency distributions of year-class strengths it should be possible to provide better advice on the probable range of variability that can be expected even if precise estimates of recruitment cannot be made for any given period.

Discussion then turned again to Pacific salmon with a focus on the utility of various modeling approaches in the face of the large variability in recruitment for given spawning stock sizes. It was noted that stochastic simulation of SR points isn't very useful when one is trying to provide year-to-year man-

agement advice. There must be some a priori model of a relationship in order to develop management recommendations. When Skeena River sockeye data are adjusted for correlations with environmental factors in Wickett's study (W. P. Wickett personal communication) there is a relatively smooth curve becoming very flat-topped in the upper half of the range, i.e. more like a Beverton–Holt curve than a Ricker curve. Although the correlations in Wickett's regression model are still intact, there is concern regarding the validity of inferences about causal effects because the correlation is much better for even years than odd years. It was further noted that the majority of studies have found much poorer correlations between environment and salmon recruitment. Finally another complication regarding salmon was observed in that the average size of fish has declined in recent years. There is some evidence that this may be a result of selective cropping of the larger spawning fish which is altering the gene pool toward smaller fish. The possibility of affecting gene pools through long-term management strategies in multispecies systems may be an important factor to consider in modeling as well as in experimental and field research programs.

Application to Fisheries Management — Case Studies

CHAIRMAN: A. T. PINHORN RAPPORTEUR: R. WELLS

This session dealt with the application of multispecies concepts to fisheries management situations. Some of the papers presented included actual models for which data had been used (e.g. Doubleday and Beacham) whereas others presented more general information on possible approaches (e.g. Tyler et al.).

Seven presentations were made and discussion followed each.

1) W. G. DOUBLEDAY AND T. BEACHAM: *Southern Gulf of St. Lawrence cod: a review of multispecies models and management advice*

In discussion, it was suggested that even if the model results fit the historical data, the test would be in the accuracy of prediction. It was pointed out that an incorrect model may predict adequately for a few years when a smoothly varying time series is involved and that a series of fluctuations in key variables is necessary to rule out this possibility. The problems of multicolinearity apparent in the model affect the estimation of optimum biomass but not short-term predictions.

There would seem to be potential difficulty for managers in interpreting complex models with respect to practical allocation problems. It was indicated that even where catches are less than total allowable catches, TACs might still be restrictive if one gear component is limited.

2) D. GRAY, D. CLAY, D. WALDRON, AND R. G. HALLIDAY: *Fishery interactions on the Scotian Shelf as a result of small-mesh gear fisheries*

In discussion it was observed that the general picture of groundfish stock recovery on the Scotian Shelf is not dissimilar from that farther south; in fact recovery seems more rapid than expected. In addition to the small-mesh gear problems, incomplete reporting of catches may have had substantial effects on calculations. It was emphasized that the accumulated effect of even small by-catches (by weight) of young cod in the small-mesh fisheries was significant.

3) S. AKENHEAD, J. CARSCADDEN, H. LEAR, G. LILLY, AND R. WELLS: *Cod–capelin interactions off northeastern Newfoundland and Labrador*

In discussion it was noted that for studies of this type, the collection of appropriate background data was necessary. Reference was made to extensive Soviet work on feeding of Atlantic cod (*Gadus morhua*) in the Barents Sea where in periods of low capelin (*Mallotus villosus*) abundance cod feed heavily on euphausids. It was also noted that on the Flemish Cap, where capelin are not present, growth rates of cod are quite high.

The possibility was raised of doing surplus energy calculations through studies of gonadal and somatic growth. Although data on fecundity are limited further analysis of changes in cod growth with respect to stock density and temperature effects may be possible.

It was noted that although estimates of fluctuations in capelin abundance prior to the 1970s are not available, anecdotal information suggests that such fluctuations were observed.

The effect of cod predation upon capelin was addressed. It was thought that cod would tend to keep low capelin biomasses low for longer than would occur in the absence of such predation. Although other predators on capelin are abundant, it is thought capelin probably have refugia from predation within cold water and the size and extent of their refugia would be affected by environmental factors.

It was not clear how the research into the cod–capelin interaction should proceed although a bioenergetics approach was suggested by some.

4) A. V. TYLER, E. L. BEALS, W. L. GABRIEL, AND W. J. OVERHOLTZ: *An alternative assemblage management approach in a mixed groundfish fishery*

In discussion, it was suggested that the target species mixes in the fishery may not be the same as the species mix determined from research surveys, and the control of species mix by fishermen may be considered as a fishing plan.

It was pointed out that some species interaction information had already been formulated and the model itself was a good example of top-down modeling. The details of the pulsed fishing plan were open to discussion with respect to the type of fishing control (effort or catch limitation) and the length of the cycles. A 6-yr cycle, for example, was considered as perhaps minimal with respect to recovery time of the fish species. The occasional and seasonal components would of course be monitored as they play a part in the stability of the system and might constitute, together with abiotic factors, driving forces. The surplus production models could be appropriate as a monitoring tool for the individual assemblage production units (APUs) and perhaps for the sum of the APUs. The determination of significant assemblage unit

change was considered difficult. To what extent the reduction of a particular species or a group of species within an assemblage is acceptable is a problem to be resolved.

This experimental approach was considered to be potentially more valuable to an understanding of the ecosystem than the mere repeated collection of data from the fishery as it presently exists.

5) D. W. WELCH: *An economic model of fishermen's behavior, and its application to multispecies fisheries management systems*

In discussion it was noted that fishermen's perception of biomass was usually a reflection of availability. The matter of by-catch is complex; instances of fishermen switching main species sought within trips and between trips were described. Considerations reflecting options for fishing were outlined, including cost of learning, distance from the stock, risk to gear, special gear for specialized fisheries, and weather considerations. In addition, not all fishermen may wish to maximize returns from the fishery. The author also noted that distribution of fishing effort in time and space is complex.

It was nevertheless suggested that an incentive–disincentive approach to management, as advocated by the author, may have some promise.

6) C. L. MITCHELL: *Economics of multispecies exploitation in fisheries: management implications*

In discussion it was noted that supply and demand tend to foster increased exploitation when biological production is reduced.

Trends in the fisheries in a multispecies context were considered more important than ill-defined optima. In the case of whales and krill, fishing pressures tend to favor the prey species because of the widely different recovery rates between prey and predator.

Benefits can probably be maximized at catch levels below maximum yield because of increased stability. The matter of time lags in ship building, capital investment, etc., in the grasping of fishing opportunities was noted, both with respect to increased and decreased resources of fish.

7) W. SILVERT AND L. M. DICKIE: *Multispecies interactions between fish and fishermen*

In discussion it was suggested that although it is likely that abundance and availability are currently confounded, in principle this problem can be resolved through a detailed knowledge of the fishery. The approach to the estimation of effort developed by the authors was felt to be theoretically sound but there is a problem in determining precisely the catchability matrix for the vulnerability of different species to different gears. It was indicated that there may be a more parsimonious way to resolve this problem.

Whither Now?

CHAIRMAN: E. J. SANDEMAN RAPPORTEUR: R. WELLS

Following a presentation by W. E. Ricker, the workshop broke up into four syndicates to consider, in light of the previous days of discussion on multispecies approaches to fisheries management advice, the implications for advice to managers today and the implications for research program planning. Separate reports were produced by each syndicate and these reports provided the basis for the general workshop discussion in the final session, which is reported below. Comprehensive agreement was not attempted and the following represents points which were agreed upon by significant numbers of participants, although not necessarily a majority.

IMPLICATIONS FOR ADVICE TO MANAGERS TODAY

In view of the wide diversity of potential management objectives and the different institutional and social constraints on management actions that are site specific, recommendations developed are necessarily very general. Nevertheless, it is noted that at least in Canada and the United States, an official mandate already exists for management on a multispecies basis. In current practice multispecies assemblages are usually managed by setting single species quotas on the dominant species in a region and forcing the fisheries to somehow find their own strategies to harvest within the framework. Within the Northwest Atlantic Fisheries Organization (NAFO) Convention Area, multispecies complications arising from single species quotas have been recognized and an attempt made to mitigate them by using a two-tier quota scheme involving catch quotas for individual stocks and a total overall catch quota for all species.

Single species and multispecies fisheries management — Although Workshop papers expressed widely divergent views on the efficacy of present single species approaches to management, it was also clear that there are examples of successful management actions based on single species concepts and that single species assessment models will continue to be of value for short-term prediction and be used for management advice into the indefinite future. Thus, it is premature to write an epitaph for single species management. Workshop participants agreed that considerable progress has been made in analyzing species and fisheries interactions and that, in particular, analyses of fisheries interactions have been used in developing improved management approaches for mixed fishery situations. It is clear that multispecies approaches to management will become increasingly important over the next decade and further into the future.

The participants considered some of the risks implied if multispecies concepts are ignored and it was stressed that three ecological principles are important in this respect.

1) Perturbations in one part of an ecosystem may be felt in other parts of the system.

2) It is likely that in most ecosystems, there are species that have disproportionately larger effects on the system for comparable changes in densities than do other species.

3) Heavy fishing pressure will tend to alter the ecosytem and the species remaining will tend to be smaller.

Situations where multispecies approaches appeared to be of particular importance were noted.

1) Fish stocks can be identified where interaction effects appear to play such a significant part that behavior of the

stocks, when standard single species management methods are applied, is totally unpredictable. Such an effect can be seen in the events that have taken place in the North Sea since 1960. Recruitment and yield of many species increased when herring and mackerel stocks were reduced. Thus, the species composition of the area changed dramatically while the total fish biomass seemed to remain relatively constant (Anon. 1979). Other examples can be seen in the concurrent increase in squid abundance with decline in the demersal stocks in the Northwest Atlantic, as well as in the Gulf of Thailand (Pope 1979).

2) Sometimes a single dominant predator–prey relationship can have such a significant influence that management advice developed separately for the exploitation of predator and prey may be erroneous. It seems likely that interactive effects between cod and capelin in NAFO Subareas 2+3K could be important in this respect (Akenhead et al. this workshop).

3) Second-order effects can sometimes be important. An example of such an effect can be seen in the kelp–sea urchin–lobster interaction. It is postulated that the significant decline in kelp biomass in some areas has been occasioned by greatly increased numbers of herbivorous sea urchins whose increased biomass is due to less predation pressure by one of their main predators, lobsters (Pringle et al. this workshop). The reduced biomass of lobsters may be due to the increased fishing pressure on the species in recent years.

If interaction effects of major species are ignored, useful advice on large-scale changes in predator stocks may not be possible and simultaneous advice on prey stock management may be unreliable because the natural mortality of prey species is affected by biomass and age (size) structure of predator stocks. When advice is based on single species assessments, management agencies should be advised that decisions to change the size of predator stocks may affect other stocks even if the effects cannot be quantified at present.

Advice for managers today — The management of fisheries is a complex process even when applied on a single species basis, and the complexities increase dramatically when multispecies management regimes are considered. The decision-making process involves a complex mix of interrelated considerations of which the biological aspects are only a part. Economic, social, and political considerations are also important and formulation of management objectives and strategies as well as the management process itself involve complex interaction among those charged with managing the fisheries, the various technical experts who provide biological, economic, marketing, and other advice, the representatives of the various levels of industry, and representatives from the political arena.

It was suggested that dialogue and mutual understanding among all the parties concerned is essential and that it is important that good consultative mechanisms be established at the earliest stages of management planning to ensure that this takes place.

The collective experience of the workshop participants indicated several specific points which many felt were important in establishing successful dialogue particularly between the "managers" and the "scientists" who provide biological advice.

Management objectives — It was suggested that in evolving successful multispecies management systems it will be necessary to develop relatively explicit statements of both short-term and long-term management objectives. Multispecies analyses (models) should assist "managers" in developing such objectives by providing insight into ecosystem perturbations that may be caused by specific management/industry actions. This suggests management–scientist dialogue at the earliest stage of management planning as well as an iterative process of redefining the management objectives as more knowledge about the evolving system is gained.

Research and development of advice — Following the definition of the short-term and long-term management objectives, the scientist can use current data and present these in a form that will best meet management needs as well as devise research programs to acquire basic knowledge where it is presently lacking.

In developing advice, the scientists should generally place emphasis on providing a series of options with their implications for different management strategies, taking into account the state-of-the-art in modeling multispecies and fisheries interactions. Likewise, scientists should attempt to indicate better the confidence limits that might be attached to their advice so that "managers" may better appreciate the level of uncertainty and its associated risk in pursuing a specific management objective. In this connection it was noted that the level of detail in scientific advice being sought by "managers" often exceeds the level that science can provide in its present state of development. This is particularly true for multispecies interactions and factors controlling recruitment.

Use of advice and the formulation of management strategies — It was widely felt that some specific comments were appropriate regarding the use of multispecies concepts and current management aspirations.

1) As a contribution to interactive dialogue between fisheries scientist and fisheries manager, scientists should make special efforts to apply current knowledge to yields from various fishery systems in the context of not being able to maximize the yield from all system components simultaneously. At this time, managers can be provided with reasonable estimates of aggregate yields from multispecies complexes for some fishery systems but it is not generally possible to specify trade-offs reliably. Current trends indicate that trade-offs will become more important as stocks recover.

2) Concern was expressed that there are major inadequacies in the present system of individual stock catch quotas which contribute to the deterioration of statistical systems. In particular, breakdown of catch and effort statistics has major implications for scientific analysis and interpretation of stocks' reactions to exploitation and short-term yield prediction and also for fisheries managers' ability to control fishery events. There are also likely feedback implications, and possible destabilization effects such as the diversion of effort from stocks in "good" condition, but underestimated, to stocks in "poorer" condition, which are overestimated. In general, alternatives to individual stock catch quotas should

be seriously examined. There was no consensus on any single preferable alternative but there was a suggestion that an effort be made to develop regulations aimed at time and place rather than being species-specific.

3) It was urged that in both current single species approaches to management and in moving toward the application of multispecies approaches, care should be taken insofar as possible not to foreclose future management options.

4) A need for greater emphasis on a systems approach to management of particular fisheries units was identified.

Implications for Research Program Planning

Introduction — Current fisheries research, targeted mainly toward the provision of advice to "managers" on a unit stock basis, emphasizes stock assessment activities and determination of biomass of selected ecosystem components. Multispecies approaches to fisheries management advice generate research needs which, though they require biomass considerations, emphasize the interactions or linkages among the components of the system and so require more complex models as well as greatly increased data requirements. To focus discussion on the research needs, we identified the following major topics which highlight some of the problems of the multispecies approach: (1) understanding the recruitment processes and the interactions that are important in the ichthyoplanktonic, juvenile, and prerecruit phases; (2) understanding the effects of predator/prey dynamics on fish growth and reproduction; (3) the need to establish a better methodology for distinguishing between biotic and abiotic effects; (4) the need to incorporate the multispecies interactions between fish and fishermen into the models and management advice.

Analytical methodology — Although the range of views on research priorities was particularly wide, the following points received considerable support.

1) Several workshop papers dealt with the analysis of highly aggregated systems. These indicate the importance of sharpening observations of fishery systems in terms of their integral behaviors. As with the Sheldon particle-size spectrum (Sheldon et al. 1972), there are a number of topics that have potential towards elucidating general system properties (Dickie and Kerr this workshop) which should be investigated.

2) Techniques for discriminating abiotic from biotic (including bioeconomic) factors in data and analyses need to be improved. The need to develop better methods for accessing and analyzing some of the large environmental databases was emphasized, as was the need to involve physical oceanographers more extensively in research teams.

3) Several main areas of increased emphasis were noted at the fishery level. Information is needed on the complex linkages among the fishery, the availability of fish, and market forces, and in particular how the fleets react to changes in abundance of species assemblages and market preferences and how these reactions affect management options. Scientists also need to know more of how individual fishing enterprises conduct their activity and the forces that govern their decision-making processes to generate the various fishing strategies employed.

4) Significant research in recent years has been devoted to ichthyoplankton surveys and attempting to understand recruitment processes. The workshop applauded this, but drew attention to the need for better understanding of the ecology of juveniles and young fish. It is in the postlarval to prerecruit stage that knowledge is particularly lacking. Often there is very little understanding of distribution and abundance of major ecosystem components and even worse understanding of feeding and mortality interactions. The stages in the life cycle when species interactions are maximal are those where biological knowledge is at a minimum.

5) The importance of groundfish surveys in estimating new year-classes and monitoring the composition of demersal fish assemblages was noted and workshop participants reemphasized the need to maintain the continuity of such traditional data series as a consistent data set. The need for extensive cross calibration was noted when changes in survey methodology become desirable. Also noted was the need for a better understanding of fishing gear behavior and the desirability of establishing improved methods for converting indices of relative abundance to absolute terms.

6) Stomach content analysis is one of the cornerstones for assessing species interactions and the workshop dealt with this topic at some length. Although research must obviously be tailored to suit the specific area being examined and the current state of knowledge of the system, many considered there was a need for some judicious combination of broad scale (temporal and spatial) mapping of fish assemblages and their feeding, with a finer scale selection of locations for detailed quantitative food web analysis. The importance of frequent periodic sampling of stomachs (of invertebrates as well as of fishes), as well as determining feeding and digestion rates, was stressed, as was the necessity of analyzing and interpreting feeding data in relation to the abundance and availability of both predator and prey species. It was also noted that a significant portion of the research programs on "food and feeding" will require aquaria and other laboratory facilities.

7) The conventional perception of the major linkages holds that predation and competition are dominant. Of these, the effects of predation are at least demonstrable in marine systems, and appropriate data are needed. Competition is a less easily defined concept, and although there is an abundance of statistical evidence for competitive interactions, if the quite narrow definition enunciated by Reynoldson and Bellamy (1972) is used, interspecific competition has yet to be rigorously demonstrated in marine fishery systems. This suggests that attention should be devoted to deriving unequivocal criteria that are appropriate for its observation in marine systems or that the concept should be reformulated in a more tractable form.

8) Fisheries interactions (linkages) tend to be investigated in relation to static terms such as biomass. The analysis of multispecies systems requires that greater attention be paid to determining rate functions (fluxes) for the transfer of energy and nutrients.

9) Analytical procedures. Workshop participants recommended increased attention to the following procedures in addition to current practices.

a) Comparative analysis, which would apply to fisheries

systems and processes established in other better understood systems (e.g. wildlife), is a potential technique that has been little utilized in the study of marine systems.

b) Analysis in terms of functional groups such as is being used by the Lake Ecosystems Working Group (Paloheimo and Regier this workshop), as opposed to more conventional taxonomic or typological approaches, is similarly underutilized. It was not urged that taxonomic approaches be abandoned, but that they be supplemented by functional analysis as appropriate.

c) Experimental management possibilities merit greater attention. A careful choice of situations suitable for experimental management could provide some clearer answers to multispecies management problems. It was emphasized, however, that clear, defensible conclusions require rigorous experimental design. Workshop participants noted that it was not necessary to experiment with the entire system and that knowledge of the requisite principles could be derived from a prototype or pilot system. An example of an innovative approach to experimental management is outlined in the paper by Tyler and his colleagues (this workshop).

Models — Mathematical modeling can play an important unifying role in planning multispecies research projects and in translating research results into practical measures. Formulating quantitative hypotheses promotes clear and disciplined thinking in the identification of relevant factors and relationships. Study of resulting quantitative models helps to identify sensitive variables which should be closely monitored in the field. Modeling of sampling programs facilitates choosing between alternative experimental designs and determining the appropriate size of the field program. Finally, simulations and projections of dynamic models assist the translation of research results into management policies and interventions.

Quantitative modeling of extensive field investigations should be carried out routinely. This type of modeling is closely linked with statistical analysis of resulting data and should be fully integrated with the field investigation. Additional modeling expertise can be called upon when a program is first set up or when major changes in direction are to be made.

Expression of scientific hypotheses in mathematical form is to be expected of research project planning. Investigations of multispecies fisheries problems, however, involve greater complexity than most marine biological investigations so that greater formalization of the modeling process and the inclusion of experienced mathematical modelers and computing experts in project planning teams is appropriate.

Data needs — Although it was not possible to examine the many specific data requirements in relation to the various research needs identified above, several principles were suggested which summarize some of the major concerns applied to data acquisition.

1) It is important that the quality and type of data required be determined through rigorous analysis, and programs must avoid getting more and more of the same types of data at the expense of obtaining the right kind of data.

2) Fisheries research currently emphasizes the distribution and abundance of species in the ecosystem with little reference to their availability to predators and fishermen. Greater emphasis should be placed on obtaining the requisite data which will allow the "availability" of stocks to be quantified in the models.

3) In keeping with the need for better recognition that the fishery is a significant part of the total system to be managed, greater emphasis should be placed on obtaining the requisite data on the fishery component. Data requirements include better information on abundance and availability of target species, fishermen's behavior in relation to changes in abundance and availability of fish as well as their response to market forces, the factors that affect the decision-making processes for fishing enterprises, and the likely reactions and adaptive behavior when different management actions are imposed.

4) Routine laboratory techniques should be applied to determining various physiological parameters for a large number of important marine species. Among the most basic parameters are standard and active metabolic levels, determined as functions of both temperature and body weight. To apply a bioenergetics approach to multispecies systems, the three primary variables (rations, metabolism, and growth) must be observed. At present metabolism is seldom estimated, rations are seldom observed in useful form (observations must be made of predator and prey sizes as well as digestion rates and maximum rations), and growth is more commonly measured as somatic growth only (and usually in the less useful term of body length). Physiological studies of somatic and organ responses to ration level and feeding frequency can be used to develop indices to analyze species interaction processes in the field.

5) In addition to the physiological parameters more information is needed on the behavioral responses of organisms, such as how physiological conditions determine the feeding rate and migration patterns of species such as cod.

Finale

Some words of wit and wisdom from Dr. Peter Larkin, Chairman of the session on fisheries interactions, at the Multispecies Workshop at St. John's, Newfoundland, November 1979.

Sometimes the fish may interact, as predator and prey,
And other times compete for food or space or come what may.
What can we say we know about such simple things as these,
What is the status of our art, what is our expertise?
Mr Pope

Sometimes the fish may not, it seems, by others be upset,
But swimming side by side at sea, die likewise in a net.
For such as these the hand of man produces complications,
And so perforce we must enquire, what are the implications?
Dr Healey

Most times the world is more complex, the puzzle more profound,

The fishes not only interact, but share a common ground,
And what is more, some fish deplore environmental stress,
The Great Lakes are the subject of our third and last address!
Dr Paloheimo

The time has come, the Chairman says, to speak of many things,
For questions, comments, loud abuse, debate that soars on wings,
So who will first essay remark, who first provide a jolt,
Will Ricker be quicker to dicker or bicker,
Or shall we hear first from Holt?

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Appendix I

Agenda

SESSION I

Introduction to the Workshop. Workshop Chairman: M. C. Mercer

Fisheries Systems Research by Canada Department of Fisheries and Oceans
Chairman: S. R. Kerr — Rapporteur: E. J. Sandeman

L. M. Dickie and S. R. Kerr: Alternative approaches to multispecies management
W. Silvert: Top-down modeling of multispecies fisheries
R. W. Sheldon, W. H. Sutcliffe Jr., and K. Drinkwater: Fish production in multispecies fisheries
P. F. Brodie and A. J. Påsche: Density-dependent condition and energetics of marine mammal populations in multispecies fisheries management

Discussion

SESSION II

Multispecies Considerations in Fisheries Research and Management Advice in the ICES Area
Chairman: S. J. Holt — Rapporteur: J. G. Pope

E. Ursin: Multispecies fish stock and yield assessment in ICES
R. Jones: Species interactions in the North Sea
J. G. Pope and B. J. Knights: Simple models of predation in multi-age multispecies fisheries for considering the estimation of fishing mortality and its effects

Discussion

SESSION III

Species Interactions

Chairman: B. E. Brown — Rapporteur: J. S. Campbell

Northeast Pacific

T. Laevastu, F. Favorite, and H. A. Larkins: Resource assessment and evaluation of the dynamics of the fishery resources in the Northeast Pacific with numerical ecosystem models
F. Favorite and T. Laevastu: Ocean migrations of salmon and estimation of carrying capacity of the North Pacific Ocean

Northwest Atlantic

M. P. Sissenwine, B. E. Brown, J. E. Palmer, R. J. Essig, and W. Smith: Empirical examination of population interactions of fishery resources off the northeastern United States
E. B. Cohen, M. D. Grosslein, M. P. Sissenwine, and F. Steimle: Energy budget of Georges Bank
J. D. Pringle, G. J. Sharp, and J. F. Caddy: Review of the interaction between carnivores, herbivores, and benthic macroalgae in the Northwest Atlantic and the implications on fishery management
T. Amaratunga: Impact of predation by *Illex illecebrosus* on the Scotian Shelf

Discussion

SESSION IV

Fisheries Interactions

Chairman: P. A. Larkin — Rapporteur: M. D. Grosslein

J. Pope and B. J. Knights: Comparison of the length distribution of all demersally caught fish combined from surveys in the North Sea and at Faroe Bank
M. Healey: Multispecies, multistock management problems in the management of Pacific salmon
J. E. Paloheimo and H. A. Regier: Ecological approaches with multispecies resources in multiple-use situations in multistressed freshwater ecosystems

Discussion

SESSION V

Application to Fisheries Management — Case Studies

Chairman: A. T. Pinhorn — Rapporteur: R. Wells

W. G. Doubleday and T. Beacham: Southern Gulf of St. Lawrence cod: review of multispecies models and management advice
D. Gray, D. Clay, D. Waldron, and R. G. Halliday: Fishery interactions on the Scotian Shelf as a result of small-mesh gear fisheries
S. Akenhead, J. Carscadden, H. Lear, G. Lilly, and R. Wells: Cod–capelin interactions off northeastern Newfoundland and Labrador
A. V. Tyler, E. L. Beals, W. L. Gabriel, and W. J. Overholtz: An alternative assemblage management approach in a mixed groundfish fishery
D. W. Welch: An economic model of fishermen's behavior, and its application to multispecies fisheries management systems
C. L. Mitchell: Economics of multispecies exploitation in fisheries: management implications
W. Silvert and L. M. Dickie: Multispecies interactions between fish and fishermen

Discussion

SESSION VI

Whither Now?

Chairman: E. J. Sandeman

Rapporteur: R. Wells

Implications for advice to managers today
Implications for research program planning

} A discussion beginning with a presentation by W. E. Ricker

Workshop breaks into three or four syndicates to prepare independent reports on the two issues

SESSION VII

Syndicates report
General discussion and wrap-up by session chairman
Concluding remarks: Workshop chairman

Appendix II

LIST OF PARTICIPANTS

S. A. Akenhead
T. Amaratunga
J. T. Anderson
T. Beacham
P. F. Brodie
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W. G. Doubleday
K. Drinkwater
W. L. Gabriel
D. F. Gray
M. D. Grosslein
R. G. Halliday
M. Healy
S. J. Holt
L. Johnson
R. Jones
S. R. Kerr
T. Laevastu
P. A. Larkin
H. A. Larkins
G. R. Lilly
L. Marshall
M. C. Mercer
R. J. Miller
R. K. Misra
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J. G. Pope
H. Powles
D. Pringle
W. E. Ricker
D. A. Roff
E. J. Sandeman
J. Schnute
D. E. Sergeant
W. Silvert
M. P. Sissenwine
S. J. Smith
M. Stocker
A. V. Tyler
E. Ursin
J. Watson
D. Welch
R. Wells

Experience of the Marine Ecology Laboratory in Relation to Multispecies Fisheries Management

S. R. KERR AND L. M. DICKIE

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KERR, S. R., AND L. M. DICKIE. 1982. Experience of the Marine Ecology Laboratory in relation to multispecies fisheries management, p. 16–17. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

The initial mandate of the Marine Ecology Laboratory was to study the processes underlying marine production, with fisheries production a major focus. The general experience of developing analyses appropriate to multispecies production systems has shown the difficulties associated with a priori descriptions based on mechanism, as opposed to the value of a selective, integral approach where system behaviors observed at a given scale are subsequently resolved into appropriate mechanisms at underlying scales.

Key words: fisheries management, productivity, ecosystems, multispecies

KERR, S. R., AND L. M. DICKIE. 1982. Experience of the Marine Ecology Laboratory in relation to multispecies fisheries management, p. 16–17. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

Le Laboratoire d'Écologie Marine avait comme mandat initial l'étude des processus sous-tendant la production marine, avec accent sur la production des pêches. La mise au point d'analyses appropriées à des systèmes de production multispécifiques a démontré les difficultés associées aux descriptions a priori fondées sur le mécanisme, par opposition à la valeur d'une approche intégrale sélective dans laquelle les comportements des systèmes observées à une échelle donnée sont ensuite résolus en des mécanismes appropriés à des échelles sous-jacentes.

IN 1965, the Fisheries Research Board of Canada founded a new biological research laboratory in association with the Bedford Institute of Oceanography. Fisheries research in Canada thereby made its first major commitment to a study of the productivity of regions from the point of view of their nature as interacting, whole ecosystems. This condition was made explicit by the chairman of the FRB, Dr F. R. Hayes, in his instruction to the new director, L. M. Dickie, that the aim was to develop a laboratory for the purpose of "studying the processes underlying marine production." Subsequent reviews of this instruction by the FRB emphasized the importance of measures of actual or potential production of fisheries as a principal index of marine production. The theme of the laboratory was therefore directly relevant to the concerns which are embodied in current language referring to "multispecies" fisheries. As was the case with the formulation by the FRB, the concern of the new language has been to understand the implications of alternative analytical approaches for fisheries yield and its management, contrasting with the historical consideration of fisheries on a species-by-species basis. The move to establish a new and separate laboratory for this purpose must be viewed as a recognition by the Board of how difficult and potentially far-reaching is the process of following a new paradigm.

The development of the Marine Ecology Laboratory is thus to be viewed initially as a consequence of a de novo commitment to a basic theme. This theme was considered important enough to be pursued virtually unrestricted by the time-lag constraints that would have been imposed by an attempt to remould the programs and staff of an existing laboratory. However, a philosophy becomes significant through the results of its application, and the development of relevance of the MEL experience to current problems must be partly traceable to the processes of staff recruitment and program formation that were set in motion.

A key early decision was the selection of St. Margaret's Bay, a relatively small prototype system, for common study and "training" by the diverse staff, some of whom had scarcely any prior knowledge or experience of marine operations or systems. In retrospect, this program also proved to be a stimulus to the developing paradigm. Emphasis of the research program was on measurement of energy transfers within the system, and description of the mechanisms on which they depended. This turned out to be a language spoken by all the scientific staff, no matter what discipline they had come from. The major lesson was that the biological production system, with its various time and space scales, had to be related to appropriate dimensions of the physical system, a requirement particularly clearly seen in relation to flushing times and the physical structure of the basin being sampled. The MEL experience showed clearly that scientists with diverse physical, biological, and mathematical backgrounds could focus effectively and work well together on specified projects of this kind.

There was a second important early realization: that it was impossible to learn all about even a small and relatively simple system. Detailed prediction for St. Margaret's Bay seemed likely to be very far in the future if it were to depend on the development of an elaborate computer description. This fact confirmed the utility if not necessity of a simpler, more holistic approach, i.e. analysis of overall performance at any scale into terms of mechanism at specified underlying scales, and the framing of testable hypotheses of action based on manipulation of parameters of the mechanisms. The core

of the MEL paradigm became that of the selective, integral approach to the analysis of complex systems, a theme that is expanded in the following two papers of the workshop. Although the papers considered here refer only to our interest in fisheries, which represents about one-third of the total MEL effort, the conclusions are consistent with the concerns of the balance of the laboratory.

The program itself resulted eventually in a number of specific findings that are clearly significant to understanding and predicting, hence managing, modern complex fisheries. The demonstration by Mann that in these north temperate latitudes basic production by macrophytes in winter and spring may have as great an impact on annual primary production as does the phytoplankton production may have especially important implications for the explanation of arctic ecosystems. Sutcliffe's demonstration that at least half of the annual nitrogen supply must come from external sources led him to consider the mechanisms of supply, and thence directly to his discovery of strong relations between estuarine circulation of the Gulf of St. Lawrence and fish production on the Atlantic coast. The results have provided major impetus for the study of long-term environmental scales in the analysis of production processes. The application of these principles to the fishery for Georges Bank, together with Mann's elucidation of the interdependance of lobsters and sea urchins on macrophyte production, were direct indices of the reality of biological species interaction in determining yield. The Georges Bank work has underlined the possibility that *horizontal* interactions may be as much a reality in the sea as Regier and his associates have shown them to be in the Great Lakes. The lobster production story provides dramatic evidence of the fineness of the balance in the *vertical* food chains, interactions that could only be suspected from previous theoretical and laboratory studies.

A particularly intriguing realization of the reality of interaction has come about in the description of what has become known as the Sheldon spectrum. The demonstration of Sheldon, Sutcliffe, and Prakash of a stability of the size spectrum in the pelagic zone over five orders of magnitude, and their finding that in this system the volume density of predators and their prey is very similar, has given rise to varied reactions, ranging from outright disbelief to attempts to use the principle to predict potential yield. The unifying power of this concept has yet to be fully explored or appreciated. Future research on the utility of the generalization at various time and space scales may produce results of direct significance to the development of multispecies management systems.

Finally, it should be noted that the attempt to comprehend fisheries as systems has led to a recognition of the importance of fishermen's behavior in the analysis of change in fisheries production. This aspect of the work stemmed from the failure of attempts by fisheries scientists in the 1960s to use catch per "unit effort" as an index of abundance. Concern with the measure was further strengthened by difficulties in the early work of the laboratory in trying to define relative abundance of the plaice stock of St. Margaret's Bay using the highly variable catch data collected by research vessel. Features of the heterogeneity of distribution of all species were evident not only in early records afforded by a research project in acoustic measurement of fish abundance, but in catches of phytoplankton and zooplankton as well. It was clear that all phases of energy transfer in the system invoked strong distribution factors, and in the case of understanding fisheries yield, required knowledge of the effectiveness of fishermen's strategies in response to distribution. A move by the laboratory in about 1970 to join the biological analyses with studies of the economics of fishermen strategies was accepted in principle by the FRB but later frustrated by government reorganizations and policy uncertainty in the face of growing criticism of the role of science in government. It is only recently that the importance of such factors in multispecies fisheries has been rediscovered. Papers dealing with the subject which appear in this workshop are long overdue.

There is one feature of the MEL approach that is notable primarily by its absence. Environmental sciences, such as the biological researches of MEL, are dependent on observations in natural systems. They thus become dependent on time series observations. The logical complement to the constraints that time series places on hypothesis testing is, of course, the comparative ecology of similar regions. Work of this sort was begun at MEL by Trites, who compared the physical dimensions and dynamics of various inlets. This background led to some initial comparisons of the impact of differing physical configurations on biological production, with particular reference to the influence of coastal inlets through export of biologically fixed materials to the continental shelf. There seems little doubt that this export includes fish larvae and larval foods, but whether or not the influence extends to other than local stocks of the coastal species remains to be determined. Some of the influence of the comparative ecological approach may be found more recently in the participation of MEL staff in a CIDA study of the Peruvian ecosystem, using methods developed for Canadian waters. However, MEL development of the comparative approach is still primarily an indication of possible direction. It would appear that work of this sort may be an important aspect of the hypothesis testing that will be required in the difficult area of understanding system stability and predicting replacement values of various species in interactive fish communities.

Alternative Approaches to Fisheries Management

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DICKIE, L. M., AND S. R. KERR. 1982. Alternative approaches to fisheries management, p. 18–23. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

Recognition of the need for a multispecies approach to fisheries management is in direct relation to the continuing trend of the industry toward greater complexity of scope, scale, and technical development. But analysis of complex systems entails determining system behaviors at appropriate levels of aggregation prior to describing the underlying dynamics: thus, the common current practice of aggregating single species models cannot succeed. Given predictors of system behavior, the managing of complex systems entails feedback information only of a complexity sufficient to accommodate the behaviors open to the system. The internal dynamics are appropriately left to equilibration through self-regulating procedures for the fishery itself. The multispecies concept embodies revolutionary implications for changes in fisheries management science, and technology, and implies the need for a reconsideration of data collections and compilation.

Key words: fisheries management, multispecies fisheries, system behaviors

DICKIE, L. M., AND S. R. KERR. 1982. Alternative approaches to fisheries management, p. 18–23. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

La reconnaissance de la nécessité d'une approche multispécifique à la gestion des pêches est en relation directe avec la tendance de l'industrie halieutique vers une plus grande complexité de portée, d'échelle et de développement technique. L'analyse de systèmes complexes nécessite toutefois de déterminer le comportement de ces systèmes aux niveaux d'agrégation appropriés avant de décrire la dynamique qui lui sert de base : c'est pourquoi l'agrégation de modèles à espèces uniques, une pratique courante, ne peut réussir. Avec des prédicteurs donnés de comportement des systèmes, la gestion de systèmes complexes implique une retour d'information dont la complexité serait juste suffisante pour tenir compte des comportements qui s'offrent au système. Il est juste que la dynamique interne soit laissée au processus autorégulateur de la pêche qui atteindra d'elle-même l'équilibre. Le concept d'espèces multiples incorpore des changements révolutionnaires dans la science de la gestion et dans la technologie de la pêche. Il comporte également la nécessité de réexaminer la collecte et la compilation des données.

Introduction

Ultimately, it is possible to conceive extreme views of what comprises a fishery. On the one hand, we might view a fishery as a particular product, landed by a specific gear, to serve a stipulated market. Alternatively, a fishery could be seen as the aggregate of all fishery products of a given socioeconomic region, in relation to world markets.

Such extremes mark limits to a spectrum of possible system definitions, any of which can have more or less relevance to the perceived social and economic problems of the day. It is a truism of systems theory that as the boundaries and scales of the system definition change, the observed structural and behavioral characteristics also change, as do the appropriate control or regulatory avenues available to the system manager. Accordingly, within this broad spectrum of possible system definitions lies a correspondingly large selection of alternative approaches to fisheries management.

Our perspective may seem overly broad in its generalized conception: it is not. The experience of the past 50 yr teaches that social perceptions, and the associated institutional organizations, are subject to rapid shifts within the possible spectrum of fishery definitions. These shifts demand flexibility and scope on the part of management. Indeed, it is no secret that we are now in the midst of a shift which is as rapid, profound, and far-reaching in its consequences as that which followed introduction of the otter trawl and nylon twine, after World War II, a shift that requires new management initiatives.

Our purpose here is to examine some portion of the available spectrum of alternative approaches to fisheries management. In doing so, we dwell in part on perspectives that have been features in the activities of our own laboratory. We offer no apologies for doing so. The organizers of this workshop, in their wisdom, asked for an account of the "MEL experience." The evaluation of alternative approaches to fisheries management has, in large part, comprised the mandate of the MEL since its inception. Thus our evident parochialism, as with that of our colleagues to follow, is offered here with slightly less than the customary measure of diffidence.

Perspective on the Multispecies Approach

A priori, it is necessary to understand the relation between the state of technical development of the fishing industry, the welter of ancillary problems, and the degree of complexity and generality of the associated management technology. It seems fair to say that management inflexibility in the past 25 yr may itself have played a major role in the chronic overfishing of many stocks, together with overcapitalized but

rundown capital resources, and rapidly accelerating management costs. Between 1970 and 1975 in particular, large segments of the world fishing industry would have suffered economic collapse in the absence of government intervention. In many respects, the history of the fisheries of the Laurentian Great Lakes affords a miniature prototype of the integral phenomenon, distinguished from the marine industry primarily in its anticipation of the full range of debilitating factors that can yet bedevil managers of marine fisheries (e.g. Regier and Hartman 1973). The need to find new conceptual models, enabling managers to reassert control and reduce waste, is great (e.g. Regier 1977; Dickie 1979a; Silvert and Dickie 1982). Our present interest in multispecies considerations has to be treated in the context of these management imperatives.

Perspective can be gained from inspection of fishery history, which suggests that various common trends may be associated in orderly patterns. Among these, we identify the following general features.

1) A most persistent and ubiquitous effect of increased fishing intensity has been the decrease in average size characterizing the mix of species landed. In part, this effect is due to the greater availability of larger fishes to conventional gears, but is also due in no small measure to the general tendency for larger species to provide the greatest per unit revenue to the fisherman (Regier 1973). Larger fishes, accordingly, are often the first to be overfished, and within species, selection for smaller size can become genetically fixed (Ricker 1972).

2) The biological property that smaller organisms are at the same time both more numerous and relatively more dispersed has required greater mobility of fishing units, together with commensurate increases in variety and complexity of the associated technology. These trends can be variously traced in, for example, the general decline of hook and line fisheries and the growth of small otter trawls, especially in association with "industrial" fishing, the intense local pressure for new technologies which would allow expansion from Nova Scotia and Newfoundland ports into northern Labrador waters, and the general developments of world-ranging pulse-fishing fleets which culminated in the Antarctic fisheries, as economic coastal control zones were instituted.

3) Because of the continuously expanding scale of marketing optima, the fishing industry itself has tended to shift from specialized, relatively narrow roles toward generalized, large-scale approaches to both the technology of supply and the creation and satisfaction of product demand. Recent tariff and marketing initiatives pursued by the Government of Canada, in consequence of extended jurisdiction, reflect the changing industrial strategy.

4) Taken together, the three foregoing considerations entail increased variety of opportunity available to the fishing industry. For both biological and economic reasons, increased variety of opportunity has encountered, and possibly exacerbated, variability of supply, which has led, in turn, to larger industrial units capable of balancing out short-term fluctuations of supply. Consolidation of the Atlantic Maritime offshore industry into virtually a single corporation illustrates our point.

The foregoing trends convey obvious implications for management science.The overriding tendency has been toward increased variety, scope, and scale of the industry itself. Our consideration here is to the appropriate response of management science to these historical trends. They will, undoubtedly, continue in the near future, and our success as managers depends directly on our abilities to recognize and accommodate to the lesson of recent history.

Inexorably, management increasingly encounters the effects predicted, in systems theoretic terms, by the "law of requisite variety" (Ashby 1956). In essence, Ashby's law stipulates that a system cannot be effectively regulated, or managed, with a lesser array of feedback information than is inherent in the range of behaviors of the system itself. Given the current trend toward increasingly complex fishery systems, it is the fact embodied in Ashby's law that has sent administrative costs spiraling, information retrieval degenerating, and enforcement, in turn, progressively less able to cope with fisherman and industry degrees of freedom. In consequence, there has been a concerted move of administration in the compensatory direction of incorporating greater generality (reducing the need for requisite variety) in its management tools.

Fisheries management began with relatively simple systems and rules which are now, quite apart from their inherent beauty and logic (e.g. Baranov 1918), rendered increasingly inadequate, of themselves, to meet the challenge of current conditions. The resulting move of administration in the direction of greater generality is represented by terms like "bioeconomic" or "multispecies" which increasingly figure in the current generation of models and management policies. It is incumbent on the management *science* underlying management technology to deal with the problems of biological species interaction in this "multispecies management" context.

An Analytical Dichotomy

We began these remarks with the extreme technical distinction between managing fisheries systems defined as single species products, or as aggregate landings in a global marketing context. Numerous alternative gradations of dimension are equally relevant. A familiar example of alternatives opposes yield-per-recruit numerical models to food-chain models. The latter class of models differs basically in that its system definition is broadened to encompass the production resource base that is dealt with implicitly, if at all, in the yield-per-recruit approach. Each approach of course can have its merits, as appropriate to the problem at hand: the essential point is that each operates with a different system definition, and will answer some questions differently (Dickie 1973). Our argument here is not so much concerned with the individual technical merits of the various possible approaches to fisheries management as it is with the appropriateness of the approaches to current perceptions of what the problems are. It has been our view that current perceptions of the management problem are forcing us inexorably toward greater generality at higher levels of aggregation, as with our present interest in multispecies analyses.

In general, there are exactly two approaches to the analysis of complex systems (Rosen 1972). Rosen identifies these as the "internal" and "external" methods of analysis; our colleague Silvert (1981, 1982) defines the modeling classi-

fication appropriate to each method as "synthetic" and "top-down" modeling. In a loose sense, these distinctions appear in the parallel ideas of reductionism versus holism, which distinction can be traced in various guises (mechanisms, vitalism, empiricism, phenomenology, etc.), doubtless to the origins of written history. The history of this basic analytical dichotomy doesn't concern us here, except to note that first one, then the other of these alternatives has enjoyed intellectual fashion, and that reductionism (internal analysis) is currently in vogue.

Although both approaches, being complementary, are essential to orderly development of management (or any) science, we argue that the current imperative cannot be satisfied without due emphasis on the external method of analysis. The case for this view is set out by Silvert (1982) and will not be provided here. Suffice it to say that the primary problems of multispecies analysis are not appropriately faced by multiplying conventional, internal models by N, as was recently done with the curiously anachronistic application of Lotka–Volterra kinetics to whale and krill populations by May et al. (1979). Although such internal analyses may remind us of the possibility of "new" properties exhibited by more complexly conceived biological systems, this approach is inherently unlikely to converge on the actual behaviors exhibited by real ecological systems (Silvert 1982; Kerr 1976; Rosen 1969).

Specifically, it is our contention that multispecies fisheries are not to be understood by more-or-less arbitrary assembly of species parts into some integral output dictated by current management interest. This may sound like a pious platitude, but its significance to management is profound. It says that management of individual species cannot properly, and should not, be undertaken out of the context of overall management of the integral production system.

This point is so frequently misunderstood, hence misapplied in both the science and technology of management as to require elaboration. Rosen (1969, 1972) has shown that the integral behaviors of complex systems cannot be usefully anticipated, *in general*, by aggregations of arbitrarily selected subsystem behaviors. In the fisheries context, however, it seems that this point is not contested so much as is the associated view that integral, multispecies fisheries possess unique behaviors in themselves. In refutation, many opposing instances could be offered, among which we list the following.

1) The overall production of freshwater fish production systems is highly predictable from basic system parameters (e.g. Ryder et al. 1974).

2) The overall production of at least some marine systems is substantially more stable than is relative production of individual species (Sutcliffe et al. 1977).

3) For many fisheries, individual species fluctuations are more strongly predicted by environmental than by fishery parameters (Fry and Watt 1957; Sutcliffe 1972, 1973; Sutcliffe et al. 1977; Loucks and Sutcliffe 1978).

4) Production may be largely independent of the detailed trophic structure of the production system, but attributes such as system size-composition may be profoundly affected (Kerr and Martin 1970; Kerr 1977, 1980).

5) Food-chain relations and community structure have greater stability than do particular realizations of species composition (Heatwole and Levins 1973; Levins and Heatwole 1973).

6) Physical (biomass) landings, although themselves relatively conservative, generally fluctuate more than do economic landings (Carlson 1975).

7) There seems to exist a general possibility of bifurcation states of system stability, rather than the continuous cline of stable states afforded in conventional models (Holling 1973; Kerr 1977).

8) The theoretical basis for the "Sheldon spectrum" of uniform size distribution in marine pelagic systems argues for generalized size-structural conservatism in all aquatic systems (Sheldon et al. 1972, 1973; Kerr 1974; Platt and Denman 1977, 1978; Sheldon et al. 1977; Silvert and Platt 1978, 1980).

Taken together, these and comparable observed conservatisms of fish production systems demonstrate the existence of emergent patterns of stable behavior at the level of multispecies associations within integral fisheries. Appropriate analysis of multispecies fisheries necessarily begins with observation of the characteristic behaviors of the integral system. In Rosen's terms, the crucial sequence is that *first* must come the phenomenological specification of macrosystem behavior, *followed* by specification of the microsystem dynamics. Otherwise, "Formalism will indeed enable you to form any averages you want, but it will not tell you what these averages mean, and which of them are useful and important in specifying and describing macrosystem behavior" (Rosen 1969).

The Current Status and Future of Multispecies Analysis

Examination of the current state of multispecies theory and analysis is a sobering exercise. In the first place, phenomenological specification of macrosystem behavior, the essential first step perceived by Rosen, is poorly developed for multispecies fisheries. Of the eight candidate conservatisms listed above, very few, if any, can be said to have been studied in proportion to their potential importance.

Appreciation of the underlying dynamics for these system behaviors is similarly impoverished. The existence of conservative behaviors by multispecies systems implies that internal interactions, e.g. predation and competition, provide the internal dynamics which merit our attention (Dickie 1972). Much has, of course, been written on these processes, but relatively little progress has been made in integrating them with observed system behaviors. Indeed, with a few singular exceptions from freshwater systems, we even lack unequivocal confirmation that competitive processes occur in marine production systems. There is an abundance of correlational support for competitive interaction in marine systems, but it is no criticism of correlation analysis to note that mere association does not in itself establish causal linkage. Reynoldson and Bellamy (1972) provide a set of five criteria, of which they consider four must be met to establish the existence of competitive interaction. To our knowledge, only the perch–trout study by Fraser (1978) substantially satisfies the criteria; and the remaining fishery evidence, for percid communities,

also comes from freshwater (Forney 1977; MacLean and Magnuson 1977). We do not suggest that it will be easy to correct our observational deficiencies, but we do insist that it is necessary to do so if we are to develop a strong technical basis for multispecies fishery management. We stress again that suitable progress cannot be made with multiple cloning of present single species models; it can only come about with deliberate intent to understand the revolutionary implications of the multispecies concept, and to conduct our research accordingly.

It is eternally risky to predict where novel research directions will lead us (if predictable, it would scarcely qualify as research). Nevertheless, on the basis of the existing, limited explorations of the multispecies paradigm, we suggest generalities that we expect to emerge, granted that we possess the will and the resources to pursue this avenue of investigation.

It may be that our current concept of food-chain processes as a discontinuous system of linkages governing discrete physical entities may be an instance of inappropriately scaled (parameterized) processes. Seen over the time and space scales of an annual fishery, the food chain may better correspond to the continuous behavior of a Sheldon spectrum of particle distribution (see references above). We need scarcely point out the simplifications that would follow if an orderly, predictable function could adequately substitute for the morass of inter- and intra-specific interactions which now complicate multispecies analysis.

Given the existence of such strong system properties as listed above, the problems associated with their practical use will focus our attention on matters not traditionally featured in fisheries analysis. Thus, following on the questions posed by Steele (1965) and Mills (1980), we shall need to understand better, for example, the following.

1) What is the pattern of behavior of the P/B ratio relative to the spatial and temporal scales appropriate to fisheries analysis (Dickie 1972)?

2) Does ecological efficiency differ in predictable ways among various functional groups in ecological systems (e.g. between cannibalistic versus predator–prey associations) (Dickie 1976)?

3) What are the biologically relevant scales of spatial variation, and how are they related to oceanographic features (Platt and Denman 1975; Kerr and Neal 1976)?

4) What is the true significance for community structure and dynamics of the additional selective mortality component imposed by a fishery?

5) Because size-related changes in ecological roles of constituent species are common, are functional descriptions of fish production systems a useful alternative to typological descriptions?

6) What criteria of "competition" can be developed that are amenable to practical measurement in the essentially unbounded marine environment? (Alternatively, is "competition" an appropriately conceived factor at present?)

7) Do recently suggested predator–prey association rules provide useful, orderly organizational characteristics for fisheries (Adams and Olver 1977; Bonar 1977; Kerr 1977; Popova and Sytina 1977)?

Lacking prescience, we are unable to do more than suggest that questions like these seem important. It requires less prescience, however, to address some likely requirements for future data collection. Clearly, the requirements for multispecies analysis differ from those now stressed for assessment purposes under the international fishery commissions. In particular, it will be necessary to relate fisheries production and yield to their appropriate natural time and space scales; and it will be equally necessary to relate observed fish catches to the various scales of environmental, oceanographic, biological, economic, and social processes rather than to arbitrarily defined statistical districts we now use. It will be necessary to resume collection and study of data on catch per unit effort. This essential index of the interaction of local density (availability) with the efficiency of fishing strategies was an unfortunate early victim of our overriding concern with the measurement of stock abundance and the "utility" of virtual population analysis (Dickie 1979b). We will also need to know some relatively simple things about the fish themselves (round weights and energy equivalents, for example) with much greater spatial and temporal resolution than is now the case. Similarly, we can no longer treat fecundity, and its energy equivalents, as the relative invariant that we often suppose it to be (Ware 1980). The potential list is long and, of course, the likelihood that we shall satisfy even the most provisional requirement depends directly on our commitment to developing a truly multispecies approach to fisheries analysis. The extant data for global fisheries is undeniably the most extensive available in any ecological discipline, a fact that has long been overlooked by the majority of ecological theorists; but in view of the enormous value of fisheries to mankind, and their immense geographic scale, there is no obvious ground for complacency. We need much better data if we are to do our job properly.

Finally, from the point of view of management, the multispecies approach calls for adaptive management at a level which recognizes effort as part of the fishery system. It is no longer sufficient to look on effort as a simple driving variable which independently and unilaterally determines the yield realized from a given stock (Loucks and Sutcliffe 1978; Silvert and Dickie 1981; Hilborn and Ledbetter 1979). Effort is determined by the complex feedback interaction of realized economic yield with market factors, capitalization, and the regulation system (Dickie 1979a). With this perspective, it becomes necessary to incorporate multispecies management into a system of "self-regulation" of the sort recognized in recent management initiatives for the Fundy herring fishery. That is, much of the current need for complexity in fisheries management, in the form of requisite variety at the level of *governmental* regulatory capacity, can be obviated by utilizing the self-regulatory capacities of the effort subsystem of the fishery. In consequence, we shall increasingly see the role of government change from that of policeman to that of supplier of information, and intervenor in market forces. It is in these directions that we believe the appropriate approaches to fisheries management now lie.

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Top-down Modeling of Multispecies Fisheries

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Management of fisheries on a multispecies basis requires comprehensive models of the complete fishery, and it is not generally possible to divide such models into distinct biological and socioeconomic components. The development of useful management models requires a sophisticated approach to the modeling process. The methodology known as "top-down modeling" is described and several examples are presented to show how this approach has been used in the analysis of fisheries and in marine ecology.

Key words: holistic models, multispecies fisheries, bioeconomics

SILVERT, W. 1982. Top-down modeling of multispecies fisheries. p. 24–27. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

Pour gérer des pêches sur base multispécifique, il faut des modèles englobant l'ensemble de la pêche, et il est généralement impossible de subdiviser de tels modèles en composantes biologiques et socio-économiques distinctes. L'élaboration d'utiles modèles de gestion nécessite une approche sophistiquée de la modélisation. Nous décrivons la méthode dite de « modélisation de haut en bas » et donnons plusieurs exemples de la façon dont cette approche a été utilisée dans l'analyse des pêches et en écologie marine.

THE transition from single species to multispecies fisheries management requires much more than the addition of some more sets of compartments to existing biological models of fish populations. Single species management has almost always involved de facto separation of the biological and economic aspects of the fishery. It is widely recognized that this separation has led to suboptimal management policies and procedures, but there has at least been a workable compromise with the fishermen fighting for larger total allowable catches (TACs) whereas the fish (acting through their representatives, the biologists) try to keep the TACs low in the name of conservation. This will not work with multispecies management. The economics of the fishery force biologists to deal with trade-offs between species and the consequent socioeconomic factors affecting exploitation rates. Thus biologists are faced with a greater change than from population dynamics to ecosystem modeling; they are forced to become involved with analysis of the entire fishery, with its many human as well as aquatic components.

Fisheries are extremely complex systems, and it is easy to build unworkably cumbersome models of them. The number of interactions within a multicompartment model is of the same order of magnitude as the square of the number of compartments, so adding a second species to a one species model increases its complexity by a factor of four, and so on. However, because we cannot expect very much precision from much models, it can be argued on information-theoretic grounds that satisfactory models of very complicated fishery systems need not actually be very complex (Silvert 1981). So long as the model reflects adequately the basic dynamics of the system, its functional form need not correspond to the degree of detail with which the system can be empirically defined.

Massive computational demands are not the only obstacles to the use of models that are constructed by synthesizing large quantities of detailed information on the components of the system. Complex systems usually exhibit collective properties that cannot be deduced by studying low levels of hierarchical structure, and most vast modeling programs have foundered on the discovery that the whole is more than the sum of its parts. Even if practically all the details are correct the complete model may be disastrously wrong (Kerr 1976), and there is no assurance that the results from a model will converge on the correct behavior even as the amount of detail becomes infinite (Silvert 1981).

The development of simple but sophisticated models requires that a large proportion of effort be devoted to such areas as system identification, sensitivity analysis, and parameter estimation, whereas the actual construction and operation of the model becomes a relatively straightforward chore. In particular, the process of system identification refers to the construction of one or more models that generate output that is at least qualitatively the same as that observed for the experimental system; it is the inverse of the usual model-building process in that the model is defined in terms of its behavior rather than the behavior being derived from solution of the equations describing the model. There exist formal techniques for system identification which are described in detail elsewhere (Kagiwada 1974; Silvert 1981), but the most important feature is recognition of system properties that may not appear when the system is viewed as simply the sum of its component parts. Such recognition often arises from simple statistical analysis of system behavior, and in some cases the identification of system properties in this way is possible even when the underlying causes of these properties are not known. This is exemplified by several

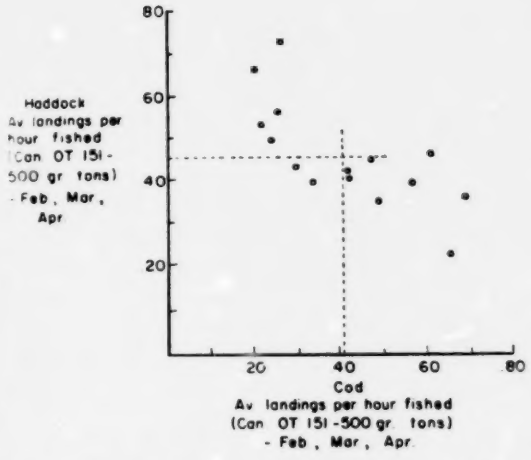

FIG. 1. Relative availability of cod and haddock to Canadian large otter trawlers in ICNAF Divisions 4V-W, Feb., Mar., Apr., 1948–62. From Dickie (1965).

studies conducted at the Marine Ecology Laboratory, which are described below.

Perhaps the simplest and clearest example of a system property in fisheries is the observation by Dickie (1965) that there is a strong inverse correlation between catch rates for cod and haddock by Canadian otter trawlers on the Scotian Shelf, shown in Fig. 1. This result clearly indicates that the total catch per hour of the two species is roughly constant and suggests that they might be combined in modeling the fishery. However, there are several possible types of models that are consistent with this behavior, and it is not clear which one is correct (Dickie 1965). In this case the top-down modeling approach does not lead to a unique representation of the system, but it does show that certain types of approaches, such as independent single species modeling, are not likely to generate reasonable simulations of the observed system behavior.

A more complex situation is represented by the observation of Sutcliffe et al. (1977) that the total fish catch in the Gulf of Maine over the period 1940–73 exhibited much less variability than one would expect on the basis of the observed variability in individual fish stocks, as illustrated in Fig. 2. This empirical observation would be virtually impossible to explain in terms of single species fisheries models, although it might be possible if one knew what one was looking for! On the basis of these observations, a simple model was constructed (Loucks and Sutcliffe 1978) that identified two basic mechanisms for the underlying covariance between catches of different stocks: differential response to environmental factors, primarily temperature, and the response of fishermen in switching from less abundant species to more abundant ones. This suggests a modeling approach based on the idea that the availability of fish (all species) is relatively constant and the fishermen are there to catch them, and the next step in the modeling process is to figure out now the *relative* abundances change from year to year; this is quite different from putting together a model based on absolute abundances of individual species.

Although the work of Dickie (1965) and Sutcliffe et al. (1977) is similar, it is worth noting that the two papers identify different (although presumably correlated) system properties, namely the relative constancy of the catch rate for two closely related species of groundfish in one case and of the total annual catch for all species in the other. Furthermore, although each study represents a significant step in our understanding of the dynamics of the fishery, in neither case do we have as yet a complete model of the fishery, nor even a firm understanding of how the observed system properties arise. What we do obtain from this type of system identification is a clear realization of the relevance of multispecies interactions in the dynamics of fisheries and an indication that total production models are likely to be of considerable value in developing the detailed understanding of the system which is our ultimate goal.

A very different type of study conducted in the same laboratory has led to a remarkably similar identification of basic system properties. Sheldon et al. (1972) observed that the particle size distribution of the oceans is quite uniform. Although the original data dealt almost entirely with microscopic planktonic particles, Sheldon and his co-workers pointed out that data on larger pelagic organisms were consistent with their observations. This work inspired a number of theoretical modeling studies based on energy flow (Kerr 1974; Platt and Denman 1977, 1978; Sheldon et al. 1977; Silvert and Platt 1978, 1980) that also predict that the total productivity of the system should be fairly constant. The remarkable aspect of this is that two entirely different analyses of fishery systems, one based on catch records and the other on plankton surveys, led to compatible submodels which may provide the basis for a comprehensive model of a multispecies fishery.

These models raise further questions which have important ramifications. For example, we can partially explain the covariance between a coldwater and a warmwater fish stock by noting that during a warm year both stocks will migrate north and the former stock will decline in observed abundance while the latter stock appears to take over. There is a sort of thermal boundary between the stocks which moves north and south with temperature. However, this model implies that the density of fish in the sea is relatively constant, even though there are different species in different environments; why is this? The question is easily answered by the evolutionary biologist, who would point out that fish evolve in such a way that available resources are optimally utilized, i.e. if there is a gap between the temperature ranges of the two stocks, they either broaden their tolerances or an opportunistic species invades. However, fishing pressure changes the environment in which fish live and adapt, so it becomes important to predict the nature of these adaptations under possible changes in fishing pressure. It is seldom possible to predict how these changes will occur on the basis of past observations, but calculations of adaptive strategy based on optimality theory are a promising way to model the most plausible response of organisms to new situations (Ware 1975, 1978).

The concept of optimality is equally applicable to the analysis of the human sector of the fishery, and optimization theory is much more widely used by economists than by biologists. The obvious tendency of fishermen to go after the most available and profitable species is a clear case of this,

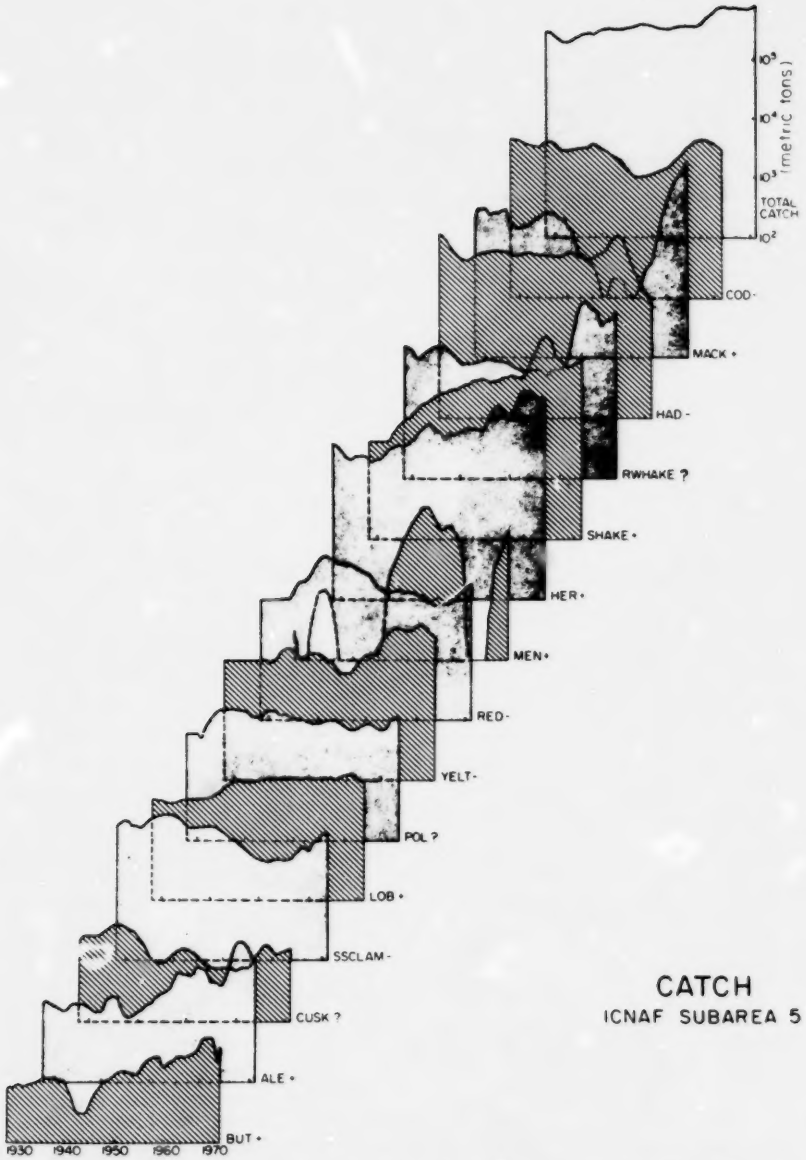

FIG. 2. Three-year running means of fish catches of various species and total from ICNAF Subarea 5. From Sutcliffe et al. (1977).

and a quantitative model of fishermen's choice based on profit maximization is described elsewhere in this volume (Silvert and Dickie 1982).

There are many techniques that can be used to identify unusual types of system behavior, and often these techniques lead to results that appear almost impossible to deduce from the properties of the component subsystems. For example, Silvert and Dickie (1982) use path analysis to show that fishing effort in the southern New England yellowtail flounder fishery appears to be a function of catch, when we would of course expect the opposite to be the case. Given the result, it appears plausible in light of the strong feedback between catch and effort (fishermen won't go after fish that aren't there), but it would require lengthy and difficult sociological research on the relationship between how much fishing a fisherman does and his success rate before we could hope to

model this feedback loop directly.

This approach to modeling, where one starts with observations on the behavior of the total system and develops a more detailed structure on the basis of these system properties, is formally known as "top-down modeling," and its implementation in marine ecology is described in greater detail elsewhere (Silvert 1981). The most important features are summarized below.

A modeling program must begin with a clearly specified set of objectives, and the director of the project must ensure that these objectives shape the design of the model. For example, most fishery scientists agree that larval survival is an important factor in population dynamics; however, prediction of larval survival does not directly fulfil the objectives of a management model. The inclusion of larval survival or other quantities of strictly biological interest must therefore be justified by system identification and sensitivity analysis.

The outputs of the model must be suitable for the objectives chosen and play an important role in determining model structure. In some fisheries the geographic distribution of the catch has important socioeconomic consequences (as in the U.S.–Canada fisheries on Georges Bank or the Newfoundland inshore–offshore cod fishery) and must be predicted, whereas geographical disaggregation would be of minor importance for the Flemish Cap fisheries.

The model architecture should be based on identification of system properties, not on preconceptions about which factors govern the system dynamics. Many system properties are counterintuitive, e.g. we may think that a predator is depleting a stock when in fact it is scavenging unhealthy individuals and improving the fitness of the survivors by reducing competition. These system properties can generally be identified by statistical analysis, as in the above examples, and the modeler then has to design a model that has these properties. In other words, instead of building a model and seeing how it behaves, the top-down modeler starts from a specification of the known behavior of the system and designs a model to mimic this behavior.

The inevitable imprecision of bioeconomic models makes it imperative to use sophisticated methods of sensitivity analysis and parameter estimation. It is important to have models provide confidence ranges as well as maximum likelihood estimators for their predictions, and managers should insist on obtaining full probability distributions for the major bioeconomic outputs and should use modern techniques of risk assessment in making fisheries decisions (Raiffa 1968; Holling 1978). Frequently the adequacy of a model can be assessed at an early stage of its development by means of a performance index based on sensitivity analysis (Silvert 1981) in conjunction with a careful estimate of the distributions of the parameters of the model (Silvert 1979; Smith 1979).

The growing interest in multispecies fishery models comes at a time when there is a strong feeling that fisheries scientists from all disciplines should be working together to analyze fisheries as comprehensive systems with interacting biological, physical, economic, and sociological components. If there is to be a revolution in the way we manage fisheries, this will require a revolution in the way we model them.

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Fish Production in Multispecies Fisheries

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Sheldon, R. W., W. H. Sutcliffe Jr., and K. Drinkwater. 1982. Fish production in multispecies fisheries, p. 28–34. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

It is possible, by relating the biomass of phytoplankton and fish, to make estimates of fish standing stocks. The advantage of this method for estimating fish stocks is that it is far easier to measure the standing stock of phytoplankton than it is to measure the standing stock of fish. If the growth rate of the fish is known then fish production and potential fishery yield can also be estimated. Fishery yields of the Gulf of St. Lawrence and the Scotian Shelf have been estimated by these methods. The predicted yields were close to the actual yields of the fisheries. This indicates that the fisheries are probably being exploited at rates that are near to the maximum for sustained production. The yield of any fishery will vary from year to year, and it is possible to estimate the magnitude of this variation and to make forecasts of the catch expected several years ahead if environmental parameters are considered. Successful forecasts have been made of the catch of the American lobster (*Homarus americanus*), and equally successful forecasts seem possible for other species.

Key words: yield predictions, biomass, size distribution, primary production, Atlantic cod, Atlantic herring, American lobster

Sheldon, R. W., W. H. Sutcliffe Jr., and K. Drinkwater. 1982. Fish production in multispecies fisheries, p. 28–34. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

En établissant la relation entre la biomasse du phytoplancton et la biomasse des poissons, il est possible d'estimer celle de ces derniers. L'avantage de cette méthode est qu'il est beaucoup plus facile de mesurer la biomasse du phytoplancton que celle des poissons. Si l'on connaît le taux de croissance des poissons, on peut alors estimer la production de poissons et le rendement potentiel de la pêche. Ces méthodes ont été utilisées pour estimer le rendement des pêches dans le golfe du Saint-Laurent et sur le plateau néo-écossais. Les rendements prédits se rapprochent des rendements actuels. On en déduit que les stocks sont probablement exploités à des taux qui se rapprochent du maximum admissible pour une production soutenue. Toute pêche aura un rendement variable d'une année à l'autre. Mais en étudiant les paramètres de l'environnement, il est possible d'estimer l'ampleur de cette variation et de prédire les prises anticipées plusieurs années à l'avance. D'exactes prévisions des prises de homard américain (*Homarus americanus*) ont été faites et il semble également possible de prédire avec succès les prises d'autres espèces.

Introduction

To determine the production of fish in any particular area it is only necessary to know their population density (standing stock) and their growth rate. Although it is not particularly difficult to measure the growth rate of fish, even though it might take time and effort to acquire the data, it is very difficult indeed to measure their standing stock. Most estimates of fish standing stocks are arrived at indirectly, usually by analyzing the age structure of commercial catches. However, a less indirect method has been proposed (Sheldon et al. 1977) in which fish standing stocks are related to those of the plankton. It seems that it is possible to establish a simple relationship between standing stock and body size when size is defined logarithmically (Kerr 1974; Sheldon et al. 1972, 1977), and that on average, phytoplankton and fish standing stocks are the same (Sheldon et al. 1977).

In an earlier study (Sheldon et al. 1977) estimates were made of the potential fish production of two multispecies fisheries: the North Sea and the Gulf of Maine. The biomass spectrum (Sheldon and Parsons 1967) was assumed to have no slope (Sheldon et al. 1972) and therefore the biomass concentration of both phytoplankton and fish was considered to be the same. To estimate fish production the size range of the fish taken by the fisheries was examined and the assumption was made that the "average" fish could be represented by a small cod, and that a production to biomass (P/B) ratio of 0.69 (i.e. doubling time, T_D, of 1 yr), which was characteristic of such a fish, was characteristic of the fishery as a whole.

Estimates of standing stock made by Sherman et al. (1978) using the methods of Sheldon et al. (1977) agreed well with observations (Sherman et al. 1978) but the estimate for the P/B ratio was probably too high (see below and also Grosslein et al. 1978; Sherman et al. 1978). The P/B ratio for North Atlantic fisheries is probably around 0.4 (T_D = 1.7 yr).

In this study we have considered the fisheries of the Gulf of St. Lawrence and the Scotian Shelf, but instead of taking an average size and an average growth rate and assuming that this was characteristic of the fishery, we have attempted to estimate the standing stock of the dominant species that make up the fishery. By considering published growth data, we then attempt estimates of fish production. In the Gulf of

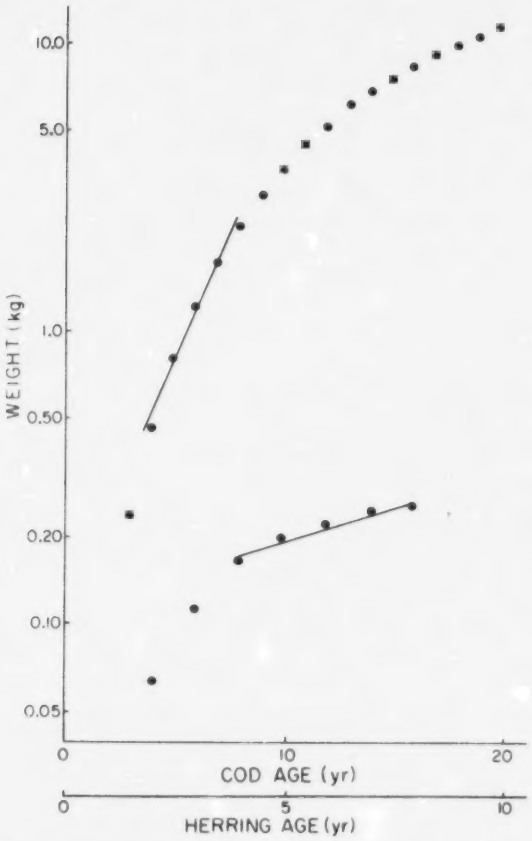

FIG. 1. Upper curve: Relationship of weight to age for cod from ICNAF area 4T (data from Ware 1980). The straight line represents the function weight (g) = 106 $e^{0.41 \text{ time (yr)}}$ and extends over the size range taken by the fishery. Lower curve: Relationship of weight to age for herring from ICNAF area 4T (data from Messieh and Tibbo 1971 and D. M. Ware personal communication). The straight line represents the function weight (g) = 112 $e^{0.11 \text{ time (yr)}}$ and extends over the size range taken by the fishery.

St. Lawrence (ICNAF areas 4R, 4S, 4T) the fishery is mainly for Atlantic cod (*Gadus morhua*) and Atlantic herring (*Clupea harengus harengus*) and to some extent for redfish (*Sebastes marinus*), but on the Scotian Shelf (ICNAF areas 4VS and 4W) there is a more diverse fishery in which cod, haddock (*Melanogrammus aeglefinus*), silver hake (*Merluccius bilinearis*), and herring are taken.

The growth rate of a fish, in common with most other organisms, varies continuously during its life. It decreases with increase of age and size. The relationship of size to age can be accurately described by some form of modified exponential function of which the logistic and Gompertz functions are but two examples (Thompson 1942, p. 155–157). However, if a fairly restricted range of age is considered the growth can be well described by a simple exponential function, particularly if weight rather than length is taken as the dependent variable.

In many cases the size range of fish taken by a fishery is not great. This is simply because small fish are not taken and large fish, although taken readily, occur at such small population densities that their biomass *in the fishery* can be neglected. For example, in Fig. 1 we give a growth curve for cod from ICNAF area 4T. The fishery mainly takes fish of between 2 and 8 yr of age (Halliday 1972) and over this age span it is not possible to differentiate between exponential and other patterns of growth. This means that, for all practical purposes, the instantaneous growth rate remains constant throughout the size range taken by the fishery and therefore simple estimates of production can be made if the standing stock is known.

The Gulf of St. Lawrence

Production in the southern Gulf of St. Lawrence is greatly influenced by water movements. Water from the Gulf of St. Lawrence flows out as a surface layer on the south side of Cabot Strait, and this is balanced by a subsurface inflow on the northern side (Trites 1970; El Sabh 1977). It follows that there is an upward displacement of deep, nutrient-rich water. One would expect this to promote relatively high levels of primary production, and measurements by Steven (1975) indicate an average production of more than 200 g $C \cdot m^{-2} \cdot yr^{-1}$.

If we use the estimates of size range and growth rate of phytoplankton given by Sheldon et al. (1977), a phytoplankton production of 200 g $C \cdot m^{-2} \cdot yr^{-1}$ represents a standing stock of 27 g $\cdot m^{-2}$ (wet weight) or 2.7 g $\cdot m^{-2}$ per size grade.[1] This is about half the average standing stock of the area off Peru (Sheldon et al. 1977). This value (2.7 g $\cdot m^{-2}$ per size grade) should also represent the standing stock of fish, subject to certain reservations (see Sheldon et al. 1977, Fig. 3). If the growth rates of the fish are known then their production can be estimated.

There are only two major fisheries in the Gulf of St. Lawrence: herring and cod. Quantities of redfish are also taken although this species does not support a major fishery. They account for less than 20% of the total catch and they have not been considered in the following discussion for reasons that are outlined below.

A summary of the phytoplankton–fish relationship is given in Fig. 2 and Table 1. The growth rates were calculated only for that part of the life span when the fish are taken by the fishery (Fig. 1). The herring (in the fishery) have a mean size[2] of 7.25 cm and occupy two size grades. The cod (in the fishery) have a mean size of 13 cm and occupy about four size grades. There is a small but insignificant amount of overlap

[1] A size grade is defined as the range of size over which the volume of an organism doubles. For example, a fish of length 1.26 cm has twice the volume (or weight) of a fish of length 1 cm. The size range 1–1.26 cm therefore represents a size grade. It should be noted that this scale is logarithmic. For a definition and a discussion of a standard size scale see Sheldon et al. (1977) and references quoted therein.

[2] To standardize size and eliminate shape factors the "size" we quote is the diameter of a sphere with the same biomass as the fish (the equivalent sphere). The actual length of the fish would be three to four times this, depending on shape.

TABLE 1. Growth and standing stock data for the Gulf of St. Lawrence. Both the standing stock and production are given in terms of wet weight.

Species	Mean size	Size range	Standing stock ($g \cdot m^{-2}$)	Growth rate	Doubling time (T_D)	Production ($g \cdot m^{-2} \cdot yr^{-1}$)
Phytoplankton	25 μm	8–80 μm	27	0.35 d^{-1}	2 d	3400
Herring	7.25 cm	6–9 cm	5.4	0.15 yr^{-1}	4.7 yr	0.81
Cod	13 cm	8–20 cm	10.8	0.41 yr^{-1}	1.7 yr	4.41

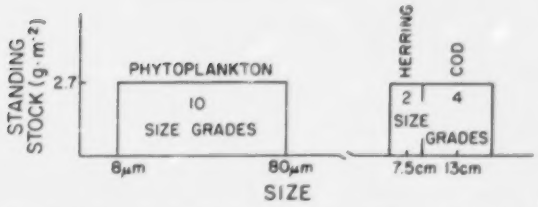

FIG. 2. Relationship between phytoplankton and fisheries in the Gulf of St. Lawrence.

between the size ranges of the cod and the herring. The fishery therefore extends over six size grades with a standing stock of 2.7 $g \cdot m^{-2}$ per size grade.

The size of redfish falls between that of herring and cod but its growth rate is very slow. It is only abundant in the cold water of the deeper parts of the Gulf. The relationship between growth rate and size is possibly temperature dependent (Sheldon et al. 1973) so that it is difficult to partition production between redfish and cod and herring as they live under different conditions of temperature. However, our estimate of redfish production (calculated in the same way as those for cod and herring below) is small (about 55 000 $t \cdot yr^{-1}$) compared with that of cod and herring, and in the interests of clarity we have not considered redfish further in our calculations. We would emphasize here that the concept of the biomass spectrum is an attempt to form a simple picture of an extremely complex set of ecological interactions, and in its present form it is justifiable to sacrifice, to some degree, precision for clarity.

The herring (or fishes of the same size) should have a total standing stock of 5.4 $g \cdot m^{-2}$. The growth constant for the herring is 0.15 yr^{-1} (this corresponds to a doubling time, T_D, of 4.7 yr) and the production is therefore 0.81 $g \cdot m^{-2} \cdot yr^{-1}$. Over the area of the Gulf of St. Lawrence (2.15×10^{11} m^2) this represents a production of 1.73×10^{11} g or 173 000 t. For the maximum sustained yield the catch should be no more than one-half of the production (Dickie 1972). A potential fishery for herring of something less than 85 000 t is therefore indicated. The current catch averages about 50 000 t (ICNAF 1958–77). This is probably close to the maximum. We have to consider that there are fish in the Gulf of St. Lawrence that are the same size as herring (e.g. mackerel) and these would have to be included in the 85 000-t estimate of fish that could be taken.

The cod (and fishes of the same size) should have a standing stock of 10.8 $g \cdot m^{-2}$. The growth constant is 0.41 yr^{-1} (T_D of 1.7 yr) which would result in a production of 4.41 $g \cdot m^{-2} \cdot yr^{-1}$. Over the area of the Gulf of St. Lawrence this would give rise to a production of 9.48×10^{11} g, or roughly 950 000 t. This would indicate that the potential fishery for cod *or fish of the same size* is not more than 475 000 t. The present fishery for cod takes about 85 000 t and the total groundfish catch is around 150 000 t (ICNAF 1958–77).

The conclusion we can draw from this analysis is that in the Gulf of St. Lawrence fish the size of herring are probably exploited at close to the maximum permissible rate, but fish the size of cod are somewhat underexploited. The management of the fish stocks that are exploited is fairly closely controlled, and if these are being fished at near to the maximum permissible rates our analysis would indicate that in the Gulf there are some fish of the size of cod that are not being taken.

The Scotian Shelf

As in many other nearshore areas of the world, primary production on the Scotian Shelf is to some extent dependent on oceanographic structure. This structure is less favorable to production than that of the Gulf of St. Lawrence and consequently phytoplankton growth is less vigorous. The outflow from the Gulf of St.Lawrence moves through the Cabot Strait and onto the Scotian Shelf. This brings nutrient-poor water to the shelf, particularly in the summer. However, as this water moves south along the shelf it mixes with nutrient-rich water from the continental slope. This results in an increase of nutrients towards the southwest. Fournier et al. (1977) suggested that this mixing might be a continuous process. The frontal region between the shelf and the slope is highly productive but the average level of primary production of the Scotian Shelf is considerably less than that of the Gulf of St. Lawrence and is probably in the region of 125 $g C \cdot m^{-2} \cdot yr^{-1}$ (Fournier et al. 1977). This would indicate an average standing stock of 1.7 g wet weight per size grade (Fig. 3).

In considering fish production on the Scotian Shelf we have limited ourselves to ICNAF areas 4W and 4VS. We had to do this because we could only make comparisons of estimated fish production to fish catch in those areas for which fisheries statistics could reasonably be applied to our work. For instance, area 4X includes the southwestern part of the Scotian Shelf, but it also includes the Bay of Fundy and it is not easy to separate catches from the southern shelf from the catch of area 4X as a whole.

The fishery of the Scotian Shelf occupies five size grades and is largely made up of four species (Fig. 3). Cod and haddock are of similar size and have similar growth rates

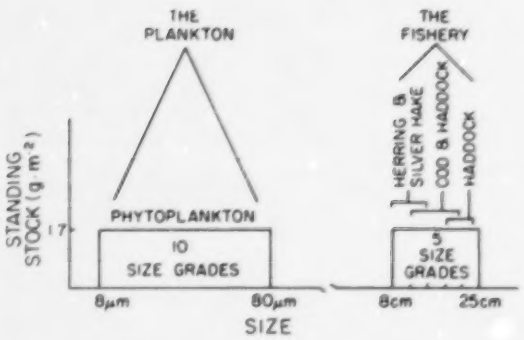

FIG. 3. Relationship between phytoplankton and fisheries on the Scotian Shelf.

TABLE 2. Growth and size data for the Scotian Shelf.

Species	Mean size	Size range	Growth rate	Doubling time (T_D)
Phytoplankton	25 μm	8–80 μm	0.35 d^{-1}	2 d
Herring	10 cm	9–12 cm	0.11 yr^{-1}	6.4 yr
Silver hake	10 cm	8–13 cm	0.32 yr^{-1}	2.2 yr
Cod	14 cm	10–20 cm	0.41 yr^{-1}	1.7 yr
Haddock	14 cm	11–18 cm	0.41 yr^{-1}	1.7 yr
Haddock	19 cm	16–23 cm	0.22 yr^{-1}	3.1 yr

(Table 2). Silver hake are smaller but have a similar growth rate to cod and haddock. Herring occupy the same size range as silver hake but they grow much more slowly (at the size at which they are taken by the fishery). Large haddock are also taken by the fishery but not in great quantities. These have a moderately slow growth rate but still grow faster than the herring. (Growth rates have been calculated from data in ICNAF Sampling Yearbooks, Vol. 10 (1967) and Vol. 16 (1972).)

Until more precise estimates of standing stock can be made there is little value in attempting to divide the fishery into too many separate units. The growth rates of the silver hake, cod, and the smaller haddock are similar enough for us to treat these three species as a unit, particularly as their size ranges overlap. These groups occupy four size grades and have an estimated standing stock of 6.8 $g \cdot m^{-2}$. Their average growth rate is 0.377 yr^{-1} (T_D = 1.8 yr) and their production would be 2.6 $g \cdot m^{-2} \cdot yr^{-1}$. The total production for an area of 8.6×10^4 km^2 would be 2.23×10^5 $t \cdot yr^{-1}$ and a fishery could be expected to take not more than 1.11×10^5 $t \cdot yr^{-1}$.

The average total finfish catch in the period 1954–62 was 1.15×10^5 $t \cdot yr^{-1}$, whereas the catch of haddock and cod alone was 0.77×10^5 $t \cdot yr^{-1}$ (ICNAF 1954–62). It would seem that during the period 1954–62 the fishery in ICNAF areas 4VS and 4W was stable with the catch being roughly equal to half the total fish production. The catches during the period 1962–77 were considerably greater (average 3.2×10^5 $t \cdot yr^{-1}$). This would seem to imply that during this time the areas were overfished and catches were being made that were greater than the production could sustain. This is similar to the situation already described for the North Sea and the Gulf of Maine (Sheldon et al. 1977).

The herring fishery presents a very different situation. If we ignore the overlap between the herring and the silver hake and assume that the herring are the only fish of their size in the fishery we can make a *maximum* estimate of the potential herring production. The herring (in the fishery) occupy 1½ size grades. Their standing stock should therefore be 2.5 $g \cdot m^{-2}$. Their growth is slow (Fig. 1, Table 2) and the production of 0.27 $g \cdot m^{-2} \cdot yr^{-1}$ is low compared with that of cod, haddock, and silver hake. The total production for the areas 4VS and 4W should therefore be 2.32×10^{10} $g \cdot yr^{-1}$ or 23 200 $t \cdot yr^{-1}$. An intensive fishery could probably take half of this: about 12 000 $t \cdot yr^{-1}$. Until 1968 catches were at about this level and it would seem that until that time the fishery was in equilibrium with the exploited herring population. But in 1969 catches soared to 111×10^3 $t \cdot yr^{-1}$. They declined rapidly from this to about 19 000 t in 1977 (ICNAF 1963–77). It would seem that during this period not only was the production taken but a substantial part of the standing stock was taken also.

Year-to-Year Variation in the Catch of Individual Species

From the above examples and from earlier work (Sheldon et al. 1977) it can be seen that it is possible to make estimates of fish biomass by using the concept of a biomass spectrum based on size, and from these estimates of standing stock one can then predict potential fish catch. However, to be useful a prediction must relate to an event from which social or economic benefit can accrue, and predictions based on the biomass spectrum suffer from one grave disadvantage: they relate to fish in terms of size, not in terms of species. For instance, we can only say that a certain weight of herring *or similar fish* can be taken each year. The similar fish could well be mackerel and it is indeed possible that there is an antipathetic relationship between the two species (Winters 1976). It is of limited practical value for a fisherman to know that a certain quantity of herring *or similar fish* will be available if the similar fish has no market value.

To a certain extent predictions of biomass available to a fishery can be augmented by forecasts of the fluctuations to be expected in the catch of individual species. For instance, in the Gulf of Maine the total fish catch remains stable from year to year at about the level one would predict from the biomass spectrum, but the catches of individual species vary considerably (Sutcliffe et al. 1977). Some variations are environmentally determined, and in the Gulf of Maine it seems that water temperature is an indicator of the factors that affect larval survival. Some species do well in cold years whereas others benefit from warm years. Because it is larval survival that is affected and because the subsequent fish catch lies some years into the future this provides a mechanism for forecasting fish catch (Loucks and Sutcliffe 1978).

By working on these principles considerable success has been achieved in forecasting the future catches of American lobster (*Homarus americanus*) in the Gulf of St. Lawrence. The effective environmental factor here is river runoff (Sutcliffe 1972). When the runoff is high the survival of the lobster larvae is also high (Sutcliffe 1973) and consequently

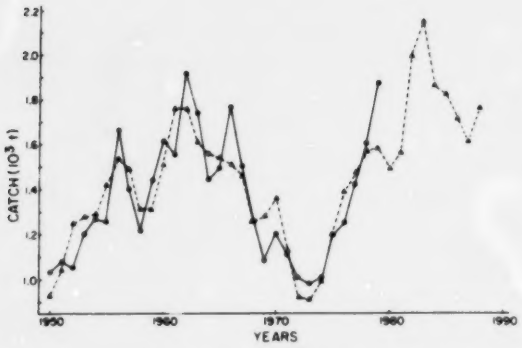

FIG. 4. Quebec lobster catch: ●—● actual, ▲. . .▲ forecast.

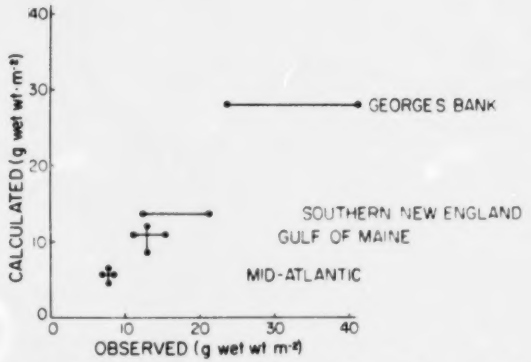

FIG. 5. Relation of observed and calculated fish standing stock. The horizontal bars represent the spread from high (1964–66) to low (1973–75) years. The vertical bars represent the range of primary production from which fish standing stock was estimated (data from Sherman et al. 1978).

the lobster catch several years later is also high.

It was originally thought that increased freshwater discharge caused nutrient enrichment and it was this that enhanced larval survival (Sutcliffe 1973). Recent studies now indicate that although nutrient enrichment does occur, an important effect of increased freshwater flow is to intensify stratification downstream with consequent retention of heat (G. L. Bugden, Bedford Institute of Oceanography, Dartmouth, N.S., personal communication). Although wind-driven mixing would have the reverse effect it now seems that in general near surface temperatures respond positively to river discharge (e.g. Sutcliffe et al. 1976).

The effects of temperature on lobster survival have received much attention (Dow 1969; Flowers and Saila 1972; Boudrealt et al. 1977), but in addition to a summer effect caused by winter runoff (Sutcliffe 1973; Trites 1970; Sutcliffe et al. 1976) a winter effect can also be recognized (Flowers and Saila 1972; Boudrealt et al. 1977). We have re-cast the relationship between the Quebec lobster catch in the Gulf of St. Lawrence and river runoff as follows:

$$C = 0.17R_1 + 0.16R_2 - 1.79$$

where C is the catch (thousands of tonnes), R_1 is the mean RIVSUM as 10^3 m^3·s^{-1} (Sutcliffe et al. 1976) for February and March, and R_2 is the mean RIVSUM for July to October, the catch being for the year in question and the RIVSUM for 9 and 10 yr previously. For the years 1950–79 this relationship explains 77% of the variation and the lag between runoff and subsequent catch permits prediction of the lobster catch until 1988 (Fig. 4). There is a suggestion that the prediction tends to underestimate both the peaks and the troughs. If the relationship holds for the future as well as it has for the past, and if there are no significant changes either in the environmental regime or in the character of the fishery then it would seem that for the next few years the Quebec lobster catch should exceed 2000 t.

Although detailed work on forecasting the catches of finfish has not yet been attempted we would expect that similar predictions could be developed for some species. For instance, the catch of yellowtail flounder (*Limanda ferruginea*) in the Gulf of Maine is inversely correlated with temperature (Sissenwine 1974; Loucks and Sutcliffe 1978). If the data base is adequate, we see no reason why it should not be possible to forecast the catches of selected species for several years ahead.

Discussion

By considering the relationship between the standing stocks of plankton and fish it seems possible to obtain information relevant to commercial fisheries. Single species pelagic fisheries are the easiest to deal with but it is also possible to make reasonable estimates of the production of multispecies continental shelf fisheries (Sheldon et al. 1977). Sherman et al. (1978) have measured standing stocks in four areas of the Atlantic seaboard of the United States and have compared these with those predicted from phytoplankton standing stocks and the biomass spectrum. The agreement between observation and theory is reasonably good (Fig. 5).

In the first attempt at relating fish to phytoplankton by means of a biomass spectrum it was assumed that an "average" fish was about the size of a small cod and a multispecies fishery occupied seven size grades (Sheldon et al. 1977). It now seems that the average fish is somewhat larger (and grows more slowly) and the fishery covers six size grades. Of these, four represent demersal fish and two represent pelagic fish. The major part of the production seems to be from the demersal fraction. The assumption of an average size of about 13 cm (equivalent spherical diameter) for demersal fish seems to work well as most of the species taken can be represented by a fish of this size and growth rate ($P/B = 0.4$). In the Gulf of St. Lawrence we estimate a potential fishery several times greater than the cod landings and this was partly confirmed by the catch statistics for fish other than cod (for which we have no growth data), whereas on the Scotian Shelf our estimates agreed well with the catch statistics. It would seem, therefore, at least for the North Atlantic fisheries, that reasonable estimates of fish production can be derived from very simple data input.

However, the accuracy of the estimates depends on predator–prey size difference (which determines the slope of

the biomass spectrum) and on measures of phytoplankton standing stock. Errors involving the slope of the spectrum are probably not important as the slope can be either positive or negative, depending on the nature of the predator–prey link (Sheldon et al. 1977), and these probably even out. We have based all our predictions on the assumption that the biomass spectrum has no significant slope. But this means that errors in the estimate of phytoplankton standing stock have a direct effect on the estimates of fish stocks.

Although there is no doubt that it is easier to measure phytoplankton standing stock than fish standing stock, it is unfortunately true that phytoplankton standing stock is not often measured. Consequently, most of our estimates have been derived secondhand from considerations of phytoplankton production and growth rates. It is also true that present methods for measuring phytoplankton standing stocks leave much to be desired. Chlorophyll concentration is often used but the relationship between chlorophyll and biomass is so imprecise that chlorophyll is a very poor index of standing stock (Strickland 1960; Loftus et al. 1972).

The use of ^{14}C to measure phytoplankton production could also lead to erroneous conclusions. In temperate waters most ^{14}C measurements are probably accurate but there is mounting evidence that production in the subtropics is grossly underestimated (Sutcliffe et al. 1970; Koblentz-Mishke and Vedernikov 1973, 1976; Sheldon et al. 1973; Sheldon and Sutcliffe 1978; Gieskes et al. 1979). This could also mean that in temperate regions phytoplankton production in summer is higher than is believed.

However, it is not easy to suggest alternatives to present methods. For standing stocks, a combination of particle counting, microscopy, and chemical analysis could perhaps be considered (Sheldon 1978). Plankton production should perhaps be measured as phytoplankton growth (Sheldon 1979). This at least would give reliable estimates of turnover. Nucleic acid concentrations could perhaps also provide information on growth rates, although as far as we know this technique has so far been applied only to animals (see Båmsted and Skjoldal 1980 and refs. quoted therein).

It is well-known that the growth rate of fish, whether expressed as population growth (Fenchel 1974) or as average individual growth (Sheldon et al. 1972), varies with size. Minnows grow faster than sharks. It is also well-known that the growth rate of an individual decreases with age. Small minnows grow faster than large minnows. But the two relationships are not the same. The growth curves for individual species are arranged *en echelon* along the average relationship (Fig. 6; see also Båmstead and Skjoldal 1980, Fig. 5). Because the fish taken by a fishery typically occupy only a small size range it is possible that a fishery exploiting large small fish will have less production available to it than one exploiting small large fish. This seems to be the situation for the cod and the herring. The herring are taken by the fishery at a size where the growth curve approaches an asymptote whereas most of the cod are taken at a size where growth is rapid (Fig. 1). This means that a much smaller proportion of the herring stock can be taken each year by the fishery than can the stock of cod. Herring might be very abundant in an area but a large proportion of the stock must be left in the sea if a fishery is to be sustained. This possibly explains why it is so easy to overfish herring stocks.

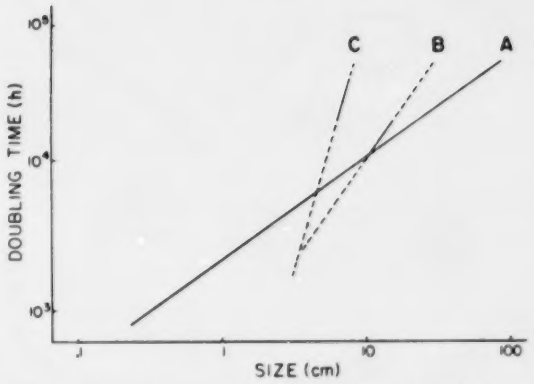

FIG. 6. Variation of growth rate with body size (equivalent spherical diameter). (A) General relationship of the form discussed by Sheldon et al. (1972) and Fenchel (1974); (B) cod from ICNAF area 4T (data from Ware 1980); (C) herring from ICNAF area 4T (data from Messieh and Tibbo 1971 and D. M. Ware personal communication). In (B) and (C) the size range taken by the fishery is shown by a continuous line (see Fig. 1 and 5).

In conclusion we would like to make quite clear that by our use of the biomass spectrum we do not mean to imply that we consider the marine food web to be either linear or simple. However, we do believe that by using size as a dominant parameter we have a very powerful mechanism for presenting a simple and robust model that averages out the complexities of the ecological interactions in the marine environment. The validity of the biomass spectrum depends on two properties: that large animals grow more slowly than small ones and that *in the sea* a predator is usually larger than its prey by a fairly constant amount (Sheldon et al. 1973, 1977). If these propositions are generally true then it must follow that the biomass spectrum is linear, and this property can be used as an aid to understanding ecological structure. Because of this simple linear function *of size*, it is possible to relate any one part of the spectrum to any other. The most interesting relationship is that between plankton and fish. We feel that even though we cannot yet define the relationship with any great precision it is still possible, with data currently available, to make useful statements about the potential biomass of fish.

However, by using size as a simplifying concept we lose precision at the species level. We can only talk about biomass at a certain size. We can say nothing about species composition or how it varies, but this problem can be addressed by looking at environmental variables. It seems that under equilibrium conditions the biomass of fish in an area is constant but environmental changes, of which temperature may be an indicator, affect larval survival and bring about changes in species composition. It is therefore theoretically possible to predict for any area (1) the average total amount of fish that could be taken by a fishery, and (2) the fluctuations within that total of the fisheries for some individual species.

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Density-dependent Condition and Energetics of Marine Mammal Populations in Multispecies Fisheries Management

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Oxygen consumption of five fasting grey seal (*Halichoerus grypus*) pups was observed over a 5-wk period. Measurements indicated an orderly sequence of tissue consumption over this period. Blubber is consumed to a heat loss threshold level above which there is a nonlinear increase in resting metabolism. Compensatory bioenergetics strategies are considered relative to individual seals within an expanding population. We conclude that, contrary to some published estimates, nonlinear increase in per capita food consumption is possible with increasing populations of marine mammals, a prospect to consider in any multispecies approach to fisheries management.

Key words: seals, energetics, populations, density dependence, feeding, heat loss, fisheries management

BRODIE, P. F., AND A. J. PÅSCHE. 1982. Density-dependent condition and energetics of marine mammal populations in multispecies fisheries management. p. 35–38. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

Nous avons observé pendant 5 semaines la consommation d'oxygène de cinq chiots de phoque gris (*Halichoerus grypus*) privés de nourriture. Les déterminations indiquent une succession ordonnée de consommation des tissus pendant cette période. La graisse est consommée jusqu'à une limite supérieure de perte calorifique au-dessus de laquelle il y a augmentation non linéaire du métabolisme de repos. Nous analysons les stratégies bioénergétiques compensatoires en regard de phoques individuels au sein d'une population en expansion. Notre conclusion, contrairement à certaines estimations contenues dans la littérature, est qu'une augmentation non linéaire de la consommation alimentaire per capita est possible dans le cas de populations de mammifères marins en expansion, facteur à considérer dans toute approche multispécifique de la gestion des pêches.

Introduction

Seals, seabirds, and whales are significant consumers of marine production, often in direct competition with fishes and fishermen. Bioenergetic analysis of multispecies fisheries requires realistic appraisal of the energy requirements of all major consumers within the production system. In particular, we need to understand how energy requirements change in response to dynamical variation of demographic parameters.

Changes in body condition and thermal balance provide important criteria of bioenergetic variation for homeotherms such as seals, because these are reflected in a cumulative effect upon the energy consumption of a stock. Estimates of the so-called "surplus" potential of fish species for commercial harvest can depend to a major degree on the energy consumption of competing mammalian predators, and multispecies management procedures must therefore allow for varying demands for prey organisms as the stocks of predatory mammals themselves vary. Clearly, the bioenergetic requirements of mammalian stocks are important considerations for multispecies approaches to fisheries management (Brodie 1975, 1977; Laws 1977; Gaskin 1978; May et al. 1979).

Two major stocks of marine mammals are now increasing in the North Atlantic. These are the grey seals (*Halichoerus grypus*) both of the western North Atlantic (Gray and Beck 1979) and the North Sea (Summers et al. 1978) plus the northwest Atlantic harp seals (*Pagophilus groenlandicus*) (Lett and Benjaminsen 1977).

There have been attempts to assess the impact upon the food base of the increase in harp seals. Winters (1975) implied that a 131% change in abundance from 1.3×10^6 to 3.0×10^6 individuals would result in a 43% increase in food consumption. This view is supported by Innes et al. (1979), who concluded that with increasing stock size in harp seals the per capita consumption of energy would be reduced. In effect, these authors conclude that increased intraspecific competition has no detrimental effect upon harp seal condition nor, therefore, upon individual energy requirements; in fact, they infer some aggregate efficiency improvement, on a per capita basis, of energy utilization for growth, maintenance, reproduction, and foraging.

In the present study we have attempted to quantify the change in energy demand with diminishing grey seal condition, measured as a reduction in blubber thickness, and we

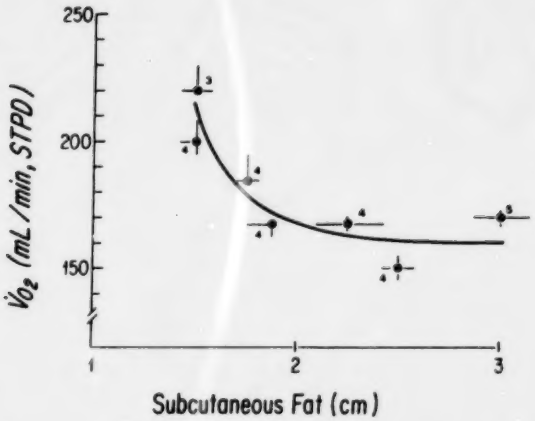

FIG. 1. Resting O_2 consumption in grey seals versus subcutaneous fat thickness during a 5-wk starvation period. Mean values ± standard errors are indicated as well as animals involved in each measurement.

consider the implications of this change for energy demands by seal stocks in general.

Materials and Methods

Grey seal pups were used in the study. Five pups, ranging from 1 to 3 wk old, were captured on the small islands off the west coast of Norway in early November 1977. These were transported to the University of Oslo and held in outdoor tanks. No food was given to the pups during the 5-wk experimental period. The pups were unrestrained in the outdoor area, being able to choose among three pools which were surrounded by resting platforms. Outdoor air temperature during this period ranged from +10 to −2°C, and pool water temperature ranged from +8 to +5°C.

At weekly intervals each seal was placed in a specially designed metabolic measurement chamber in which it was immersed with only the head exposed (water temperature 7 ± 1°C). A description of the chamber and methodology appears in Øritsland et al. (1982). The seal pups were not otherwise restrained, and O_2 consumption measurements were taken only when they were observed to be inactive. At the end of each weekly trial, the seals were weighed, and sternal blubber thickness was measured by ultrasonic techniques (Kretz Technik, Impulse/Echogerat, #24ME within 10% accuracy ± 0.25 cm). The results (Fig. 1) are plotted as mean values ± standard error. Student's *t*-test was used to determine significant differences between means. Weights of the pups are given in Øritsland et al. (1982).

Results

There were initial differences in blubber thicknesses among the five animals used in this study; therefore each point in Fig. 1 does not always represent five animals. The trend to increased O_2 consumption with decreased blubber thickness was demonstrated by following individuals through a period of blubber reduction and, as shown in the figure, was further demonstrated by the cumulative data.

Reduction in blubber thickness from 3 to 2 cm caused no significant change in resting O_2 consumption (Fig. 1). However, a further reduction from 2 to 1.5 cm of blubber thickness resulted in a significant increase ($P < 0.025$) in resting metabolism (of the order of 40% increase in O_2 consumption).

During the 5-wk experimental period there were notable changes in behavior. One change, which could be interpreted as a response to heat loss, was that as an apparent threshold in heat loss or blubber thickness was reached, the seals hauled out on the platform. Such a change in behavior would reduce heat loss. There was a sequence in this response, with the most emaciated pups hauling out first. Similar behavior was observed in common seal (*Phoca vitulina*) retained in open system seawater at Bedford Institute in 1971 (P. F. Brodie unpublished observation).

Discussion

It is apparent from this study that decrease beyond a critical blubber thickness results in a nonlinear increase in metabolic rate. These observations agree with the Irving and Hart (1957) experiments on *Phoca vitulina*. These authors found that a "stunted and skinny" seal had a resting metabolic rate 50% greater at 20°C than another of the same age but superior fat thickness.

The observed reduction in blubber thickness during starvation is consistent with the findings of Sivertsen (1941) and Chapskii (1964). Øritsland et al. (1982), studying metabolic rates of grey seals, found for one individual with blubber thickness of 3.5 cm that assuming a caloric equivalent of 7200 kcal·kg^{-1} (3.0125×10^4 J·kg^{-1}) produced an acceptable simulation of the observed weight loss; but for an animal with blubber thickness of 1.9 cm, the caloric equivalent had to be only 3900 kcal·kg^{-1} (1.6318×10^4 J·kg^{-1}). From the higher caloric values indicated for thick blubber, it would appear that at the initial stage of blubber reduction, lipids are a major source of energy. But once blubber is reduced below some critical thickness, it appears that the thermoregulatory needs of seals require that fat be conserved. To provide an alternate source of energy, a shift to utilization of body core tissue, primarily protein, is indicated by the reduced energy density that was observed.

Initial consumption of blubber was considered the first response in a feeding reduction experiment by Bigg et al. (1978). Similarly, Pernia et al. (1979) found fat consumption was an initial priority for fasting northern elephant seals. It is anomolous that the studies of Stewart and Lavigne (1979) on harp seals did not find this to be the case. They found no significant change in fat thickness with starvation, but a 35% reduction in body core weight. To them, this implied that there was no fat consumption indicated and that muscle was consumed in the initial phases of starvation. Estimation of energy storage or consumption rate by measuring body core weight (Stewart and Lavigne 1979), rather than caloric content, may be confounded with changes in water content and fat protein composition, as demonstrated by Bintz et al. (1979).

Based on the above findings, we posit the following sequence of tissue utilization during a starvation period:

(1) utilization of fat nodules, if present around internal organs; (2) utilization of a portion of the insulative blubber to a critical minimum thickness; (3) utilization, in part, of the muscle core; and (4) as a final resort, utilization of the remaining blubber layer. (A seal in such a critical state would presumably not consume its propulsive tissue to the point of eliminating its effectiveness as a predator, but at some point it would shift back to utilizing its remaining blubber insulation.) In fasting, some muscle is consumed to provide glucose (Brodie 1975).

When we apply our findings to an expanding seal population we find them inconsistent with the conclusions of Winters (1975) and Innes et al. (1979). We take this view for the following reasons. An increasing seal stock must at some level of abundance encounter a reduced per capita availability of prey, due to increased intraspecific competition. In consequence, either blubber reserves should decrease, on average, due to lower food intake, or if blubber thickness is maintained, foraging costs must increase. As we have shown (Fig. 1), decreasing blubber reserves below a certain threshold further exacerbates energy requirements because of the increased cost of thermoregulation. Taken together, we view these factors as arguing for a proportionately greater energy requirement by large, increasing seal herds; certainly we find no grounds for the view that large herds could exhibit proportionately greater energy efficiency, once beyond some initial levels of increased abundance.

Detailed appraisals of seal energy budgets are, of course, complicated by many associated considerations, and quantification is correspondingly difficult. It is useful to consider two major avenues of bioenergetic response open to seals encountering increased intraspecific competition for prey resources.

Foraging Effort

There are differences in migratory and feeding behaviors among seal species, e.g. solitary feeding by grey seals, as opposed to the schooling or formation swimming behavior observed of migrating and feeding harp seals. With the latter, an increase in stock size could result in an increase in the number of groups rather than in seal numbers within individual groups. Differences such as these should affect the spatial characteristics of a stock's interaction with its prey resource, modifying the stock abundances at which individuals experience the relative effects of competition for food.

Similar consequences could follow from changes in migratory behavior (Sergeant 1973; Bowen and Sergeant 1979). The question is whether increased seal abundance can be offset by restricted migration, in part at least, by feeding on local prey rather than making extensive migrations to areas of seasonal high production. But migratory patterns have presumably evolved optimally, with selection for areas of maximum prey availability (Sergeant 1973; Jangaard 1974; Schul'man 1974; Brodie 1977), and it is difficult to conceive that changed migratory patterns could often provide increased foraging efficiency for a stock. Accordingly, we find no reason to believe that changed spatial utilization of available prey could in general sustain increased foraging efficiencies in the face of enhanced resource competition.

Thermal Maintenance

Of all aspects of the marine mammal energy budget, the costs of thermoneutrality seem the highest, with the possible exception of the lactation period (Lockyer 1978). With an increase in a marine mammal stock there is essentially that much more mammalian surface area exposed to a cold marine environment. In the case of the harp seal, an increase of 131% in stock size (Winters 1975; Innes et al. 1979) would mean that the total surface area would be more than doubled. This estimate is conservative, as a large stock would tend to accumulate larger, older animals. Hauling out, as observed in the laboratory experiments discussed above, represents a possible, compensatory behavior, but this is at best a short-term solution to thermal maintenance. Furthermore, with an increasing stock size there would eventually be a higher frequency of individuals approaching critical insulation quality levels, based on our findings. But even where blubber thickness is maintained beyond the critical threshold for thermoregulatory efficiency, this will not reflect the increased foraging effort and associated energy consumption required to maintain adequate blubber reserves.

Finally, we should remember that the aforementioned increases in harp seal stocks will take place in the face of intensive competition by the commercial fisheries for similar prey (Brodie 1977), further exacerbating the effects of intraspecific competition. In general, therefore, we question the hypothesis that per capita consumption of energy decreases with an increasing stock of marine homeotherms. We suggest that there are sufficient grounds to reach the opposite conclusion. In the context of multispecies management, consideration should be given to the possibility that there is a nonlinear increase in both individual and aggregate energy utilization as stock abundance increases. This is a major potential effect that should not be overlooked in the multispecies management context.

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Multispecies Fish Stock and Yield Assessment in ICES

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URSIN, E. 1982. Multispecies fish stock and yield assessment in ICES, p. 39–47. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

Accumulating information on the extent of predation upon fish stocks suggests a consideration of predation patterns before recommending major changes of predator stock sizes. Methods of multispecies assessment are discussed and the results of single species and multispecies assessments for North Sea cod (*Gadus morhua*) are compared as an example. Differences between the two methods are due as much to changes in the age structure of predator stocks as to changes in biomass. A perhaps feasible way of introducing multispecies assessment into ICES working groups is suggested.

Key words: yield, assessment, population dynamics, fishery management, species interaction, predation, cod

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Les connaissances qui s'accumulent sur l'étendue de la prédation sur des stocks de poissons donnent à penser qu'il faudrait considérer les caractéristiques de cette predation avant de recommander des changements majeurs aux effectifs des stocks prédateurs. Nous analysons les méthodes d'évaluation multispécifique. À titre d'exemple, nous comparons les résultats d'évaluations monospécifiques et multispécifiques de la morue franche (*Gadus morhua*) de la mer du Nord. Les différences observées entre les deux méthodes résultent autant de changements dans la structure par âge des stocks prédateurs que dans la biomasse. Nous suggérons un moyen peut-être applicable d'introduire l'évaluation multispécifique parmi les groupes de travail du CIEM.

Present Single Species Assessments

The advice on fishery management given by ICES (International Council for the Exploration of the Sea) to various international bodies (North-East Atlantic Fisheries Commission, International Baltic Sea Fishery Commission, European Economic Community) is based on single species stock and yield assessment. The principal methods are the Beverton and Holt (1957) yield per recruit model and various cohort models, particularly so-called virtual population analysis (VPA), which are logically consistent with the Beverton and Holt model. The cohort methods estimate recruitment, and in their original form calculate backward in time. Calculating forward in time requires recruitment parameters or the numbers of recruits as inputs. Calculating backward requires an estimate of either the fishing mortality coefficient F or the number in the population for the oldest age-group of each cohort.

Species Interaction

The Beverton and Holt model and cohort analysis have both been used as foundations for multispecies methods, none of which have so far been used for advisory purposes. The kind of interaction dealt with is between F and M, the coefficients of fishing and natural mortalities. F_i influences the stock size of species i, whose predation influences the natural mortality of the prey species among which species i may be itself. An additional kind of species interaction, namely the interaction between F values, occurs when several species are caught in the same gear.

The dependence of M upon F has been discussed in a small number of ICES papers read since 1973 and particularly in 1979. We shall return to these later. Except in 1979 they have not influenced ICES working group reports and they have only sporadically influenced the advice issued by ICES through the Advisory Committee on Fishery Management (ACFM). It nevertheless seems unavoidable that assessment workers shall devote increasingly more time to the study of species interaction because of the overwhelming evidence gathered in recent years on the large quantities of fish, relative to landings, consumed by fish and other marine animals. As we shall see later, such figures may lead to overestimating the influence of predators upon the fishery.

Fish Consumption by Predator Populations

Most information on the size of fish populations is of recent date and investigations on food consumption by populations remain remarkably scarce. As well, data on population size and food consumption are not often as reliable as they ought to be.

The main theme of this paper is the dynamics of the North Sea fish stocks. It is therefore important to note that a particularly thorough investigation of the fish consumption by North Sea cod (*Gadus morhua*) was published by Daan (1973, 1975). There is much uncertainty involved in the estimation of the food consumption of a single cod. Jones (1978a) calculated consumption by two different methods, both giving higher values (as shown by Sparre 1979) than found by Daan. At the present time it seems wise not to overestimate preda-

tion; the feeding rates calculated by Daan are therefore used.

Daan estimated that in 1967–70 there was a stock of 336 000 t (metric tonnes) of cod in the southern and central North Sea. They consumed 1015 000 t per year, 359 000 t of which were species designated by Daan as "commercial fish." These were mackerel (*Scomber scombrus*), whiting (*Merlangius merlangus*), haddock (*Melanogrammus aeglefinus*), herring (*Clupea harengus*), plaice (*Pleuronectes platessa*), and sole (*Solea solea*). Comparison of percentage total fish and percentage commercial fish in the stomachs (Daan 1973, Tables 3–7) shows that commercial fish did not exceed 70% of total fish and perhaps not even 50%. In other words, cod consumed 500 000–700 000 t fish per year. The "noncommercial" species (probably mainly sand eels (*Ammodytes* sp.), Norway pout (*Trisopterus esmarki*), and sprat (*Sprattus sprattus*)) are subject to extensive fishing for processing. These investigations covered less than two-thirds of the North Sea. On the other hand, the biomass estimates are high as compared with estimates by the ICES roundfish working group in its report for 1978. To obtain a cautious (low) estimate we modify the figures to cover the stock size calculated by the working group for 1977. This stock estimate is about 215 000 t. Making another cautious estimate by assuming commercial fish to be 70% of total fish consumed we have:

Cod biomass			215 000 t
Cod food			650 000 t
Invertebrates		320 000 t	
Fish		330 000 t	
Commercial	230 000 t		
Noncommercial	100 000 t		
Food consumed per tonne cod per year			3.0 t

The commercial fish are medium-sized to large species with a mean weight (in the cod stomachs) of 40 g. Their biomass might have increased by a factor 2 or 3 even considering natural mortality, if they had not been consumed.

On the other hand, these fish would themselves have consumed some fish which are spared because their potential predators fall prey to cod. Such considerations tend to get involved, particularly when there are, as in the North Sea, a dozen important fish species all more or less interacting with each other. Some mathematical modeling is needed, supplementary to the traditional single species models. Before continuing the argument on species interaction it therefore seems pertinent to discuss the basic principles of some multispecies assessment models.

Multispecies Models

A full discussion of the subject could involve all kinds of aquatic ecosystem models, but this short overview is confined to a few models or families of models intended for fishery management purposes. We shall focus on the parameters of species interaction.

One family of models has interaction parameters of the Lotka–Volterra type. They describe the positive or negative magnitude of the interaction without specifying the biological background of the interaction. Examples are the Leslie matrix model of Pope (1976) and the multispecies Schaefer model (Larkin 1963; Walters and Hogman 1971; Pope 1979a). Such models are mathematically neat, but the parameter estimation presents problems which remain unsolved. In a two species case some reasoning about the biology of the species may provide an estimate of the magnitude and sign of the interaction parameters.

With a fair set of data the parameters can be formally estimated. Just as when two parameters are estimated from the slope and Y-intercept of a straight line, there is a risk of introducing a correlation in the estimation process. In the case of a straight line an accidentally steep positive slope is automatically accompanied by a low intercept value. This is worse when many parameters are estimated in the same process. With many interacting species, the individual parameter estimates may become biologically meaningless (negative when expected positive, etc.) even though the fit to data is good. Such estimates are dangerous to use in predictions and, accordingly, the credibility level of models of this kind is low.

A second family of models is characterized by an explicit description of food consumption which makes the species interaction more transparent to a biologist. Riffenburgh (1969) seems to be the first author to develop a multispecies assessment model of this type, a study of the interaction of hake (*Merluccius productus*), anchovy (*Engraulis mordax*), and sardine (*Sardinops sagax*) on the Pacific coast of North America. It was tentatively implemented for the North Sea by Agger and Nielsen (1972), probably the first attempt towards species interaction assessment in Europe. The backbone of the model is a transition matrix of probabilities of transfer from one entity in the model to any other entity (for instance, 0-group sardines to either I-group sardines or hake). The probabilities add up to one for the transfer of each entity and are calculated once and for all when the computation begins, based on original biomass values. This can be disastrous to the result because the purpose is to calculate the effects of altering the biomasses by changing the effort. For instance, the consumption of sardines by hake is proportional to sardine biomass, but independent of hake biomass which is a dubious approach to analyzing the influence of hake upon sardines.

Laevastu and Favorite (1978, unpublished reports and this volume) developed an extensive ecosystem and fish stock assessment model existing in several versions of various degrees of complexity. The description of food composition is based on percentage contribution of prey species or age-groups from analyzing stomach contents. This food composition is a function of the predators' preferences and the biomass of each prey when the stomachs were collected. If, in a simulation, a prey becomes scarce, some arbitrary action must be taken to prevent it from being consumed to extinction.

The models remaining to be described (Pope 1979b and this volume; Helgason and Gislason 1979; Andersen and Ursin 1977) handle food consumption better and are similar in the way percentage food composition is calculated. They are extensions to the Beverton and Holt model and to cohort analysis. In these models the food of a predator is partitioned among the potential prey species in proportion to each prey biomass weighted by a coefficient indicating its suitability as food for the predator or, looking at it another way, the ability

of the predator to find and eat the prey. Formalizing, we use the index i to indicate a predator and j to indicate a prey. The biomass of j is B_j and its suitability as prey for i is G_{ij}, G taking on values between zero and one. The j biomass available as food for i becomes

$$\varphi_{ij} = G_{ij}B_j$$

and the total food available to i is

$$\varphi_i = \sum_j \varphi_{ij}$$

where j runs over all the entities (species or age-groups) in the system, so that the fraction of j in i's food becomes

$$p_{ij} = \frac{\varphi_{ij}}{\varphi_i}$$

Trophic levels are not defined because both i and j run over all entities even though entire rows or columns of the φ_{ij} array may be zero. The array of G_{ij} values establishes a sort of trophic hierarchy. The problem of determining G_{ij} values is discussed in a later paragraph.

With information on total food consumption per specimen in each entity in the time step, an array N_iR_{ij} of food consumed can be established (N_i, number of predator i; R_{ij}, grams of prey j in the ration of i). Summing over j (the prey) gives the consumption by each kind of predator. Summing over i (the predators) gives the "yields" taken by predators other than man. Although recently ridiculed by Gulland (1979) this seems an efficient and perhaps the only rational way of calculating death by predation.

The multispecies cohort model of Pope (1979b and this volume) is the simplest model using the above method of calculating food consumption and predation mortality. Pope uses his own extremely simple cohort analysis (Pope 1972) and the description of species interaction is reduced to the bare essentials and perhaps a little less. A fraction (fixed for each predator) of the food is obtained from species not represented in the model. The remainder is partitioned upon prey species as described above. Difficulties arise if the biomass of species mainly serving as prey is depleted by predators or by man. The predators continue to take the same fraction of their food from the already depleted prey species included in the analysis which may be disastrous to prey stocks. This can be overcome by defining the "other food" not as a percentage of the food of each species included, but as one constant biomass weighted by a G value specific to each kind of predator. This quantity would be added to the denominator before calculating the fractions p_{ij} of j in the food of i. This was done by Helgason and Gislason (1979).

A more serious problem in Pope's (1979b) model is the cursory treatment of the 0-group. Cohort analysis deals with numbers. To determine the food value of a specimen a body weight must be assigned to it. This presents particular problems for the 0-group which grows from less than a milligram to 10 or even 100 g before being admitted to the 1-group. The choice of mean size when preyed upon by a given predator is of paramount importance to the result. In Pope's own exercise with six North Sea fish stocks there is a suspicious concentration of predation upon 0-group fish, perhaps indicating that the mean weights of the 0-groups were chosen too high. Another problem is that 0-group numbers are purely formal. They are calculated backwards to January 1 of the year in which the fish are born because present yield statistics are by calendar year.

Suitable values of 0-group body weight can be estimated only when stomach analyses by age-group of predator are available specifying the contribution by age-group of each species of prey considered. Such analyses must be carried out in years covered by the cohort analyses.

Helgason and Gislason (1979) use VPA, which is more robust than Pope's cohort analysis for high mortality rates. They also include more detail, particularly with respect to juveniles, using differential equations for growth and mortality. Both models assume constant size at age: growth and food consumption rates are constant and independent of food concentrations. This raises a problem of logical consistence. The ordinary backward calculation of a cohort analysis gives no trouble because the population sizes necessary to make up for mortality are created automatically. Convergence of the iteration in the predictive phase when calculations are forward in time requires the constraint that total food available is constant. This assumption is consistent with those already made that growth and consumption rates are constant.

Designating the "other food" (food not included in the cohort analyses) available to species/age-group i by φ_{io}, we require

$$\varphi_i = \sum \varphi_{ij} + \varphi_{io} = \Phi_i \quad (\Phi_i \text{ constant})$$

Analysis of stomach contents of i gives the fraction p_{io} of "other food" in the diet in the year in which stomachs were sampled. We have

$$p_{io} = \frac{\varphi_{io}}{\sum_j \varphi_{ij} + \varphi_{io}} = \frac{\varphi_{io}}{\Phi_i}$$

from which

$$\varphi_{io} = \frac{p_{io} \sum \varphi_{ij}}{1 - p_{io}}$$

Once determined, Φ_i becomes a parameter and we have in consecutive calculations

$$\varphi_{io} = \Phi_i - \sum_j \varphi_{ij}$$

Thus, a reduction of the size of some stocks included in the cohort analysis will not lead to increased predation mortality rates in a self-accelerating process as when predators are allowed to hunt at an increasing speed trying to obtain their usual share of declining prey stocks. This is what particularly Pope but also to some extent Helgason and Gislason let them do, with the eventual severe depletion of certain stocks as a result.

Andersen and Ursin (1977) present the most detailed and probably the most robust of these models. The calculation is forward in time and based on the differential equations of Beverton and Holt plus one for the rate of feeding. Food selection is as in the other models of this group, but a "half-saturation constant" is introduced. This makes food consumption and growth functions of food concentration. The numerical integration process and the half-saturation constant together ensure that nothing is consumed which is not present and that growth does not come of nothing. The constant food consumption of an entity in the two other models is here represented by a maximum food consumption. The actual food consumption is the maximum multiplied by a coefficient f (the feeding level) ranging from zero to one. The feeding level of species i is determined by

$$f_i = \frac{\varphi_i}{\varphi_i + Q}$$

where φ_i is the food available to i. The half-saturation constant Q must at present be estimated by trial in the model. The predators cannot find food and starve when Q is too high. When Q is too low they eat all the food and starve afterwards. With an intermediate Q value they eat prudently without depleting the prey stocks. The reliability of the Q estimate depends upon the data available for comparison with calculated values for a number of years (yield, age frequency distributions, growth rates, stomach contents, etc.). Extreme perturbations of the system in the period covered, caused by changes in fishing patterns or in year-class strengths, reduce the risk that the solution found is one of many possible. The risk that the user of the model fiddles with parameter values until finding a solution agreeing with his prior prejudice is difficult to evaluate. With a many species system and an abundance of data as in the North Sea application referred to below, it seems a hopeless task to find several sets of parameter values which when used for predictions would lead to markedly different results. An exception is the estimation of recruitment parameters (see section on single species and multispecies assessment for North Sea cod).

Pope's (1979b) model was applied to a system of six fish species in the North Sea. No application of the Helgason–Gislason model is published yet, but a North Sea exercise is under way (H. Gislason, Danish Institute for Fisheries and Marine Research, Charlottenlund Slot, DK 2920 Charlottenlund, Denmark, personal communication). Assessments with the Andersen–Ursin model were made for sprat, herring, and cod in the Baltic by Mandecki (1976) and Majkowski (1977), both using an early manuscript by Andersen and Ursin. Lassen (1979) applied it as a two species model to sprat and cod in the Baltic, using a first-order approximation to the differential quotients: a gain of simplicity paid for by loss of robustness. Andersen and Ursin (1977) and Ursin (1977, 1978) made assessments for 10 important fisheries in the North Sea.

It is difficult to rank these models with respect to credibility. Going from Pope (1979b) via Helgason and Gislason (1979) to Andersen and Ursin (1977) we find a loss of simplicity and a gain of flexibility and robustness against major perturbations. A simpler model is easier to accept but has a more limited field of application.

The discussion has so far passed lightly by the contents of the array G_{ij} describing the suitability of any prey to any predator, which is described in the following section.

The Problem of Describing Vulnerability to Predation

Conveniently, vulnerability to predation is described similarly in the models of Pope (1979b), Helgason and Gislason (1979), and Andersen and Ursin (1977). Elements of the vulnerability, or suitability, array G_{ij} may be allotted values ranging from zero to one. The considerations behind the construction of such an array are more or less independent of the model in which it is used. Unfortunately, the G array was leniently treated by all authors, but its development will be an essential exercise in multispecies assessment work of this kind. When properly established for an area the G array is a summary of a substantial part of the present knowledge of the biology of the various life stages of the species involved, their distribution, behavior, and feeding habits.

The rational thing to do in an analytical approach is probably to make G the product of three coefficients (arrays), each taking on values between zero and one. One array describes the suitability of the prey with respect to size, the next the fractional overlap of the distribution in space and time of predator and prey within the sea area considered, and the third describes the chance of encounter due to the behavior of predator and prey (pelagic or demersal, hidden in sand, fast or slow moving). Keeping separate the three subjects (size, distribution, and behavior) prevents confusion and makes it easy to incorporate new information.

For example, Andersen and Ursin (1977) tentatively reduced the G values for cod eating herring because herring are fast swimmers and heavily schooling. Recently, Bagge (1979) found in the Sound between Denmark and Sweden that young cod fed mainly on small herring and sprat while large cod took fewer herring although big herring were plentiful. They consumed more flatfish and young cod of suitable size instead and seem to have achieved a lower feeding level than small cod. A simple explanation is that big herring swim too fast for the cod. This could be introduced into a species interaction model by making the behavior coefficients for cod preying upon herring a decreasing function of cod age.

Frequent stomach analyses are necessary as a check on the realism of the elements of the arrays. A purely empirical approach to the estimation of the G array is possible when stomach analyses by species and age-groups of prey are available for all species and age-groups included in the cohort analysis (Sparre 1980).

First Steps Toward Multispecies Assessment in ICES

The accumulating evidence of large quantities of fish being consumed by fish and other marine animals has had little effect on management. The multispecies assessment papers I have referred to above were mostly neglected as were three papers on species interaction in more general terms (Jones and Richards 1976; Jones 1977, 1978b). Yet, there is some development in 1979.

An ad hoc working group on interaction between grey seals (*Halichoerus grypus*) and fish stocks (Anon. 1979a) found that by decreasing the seal stock, fishing would gain more than the fish consumption by seals was reduced. At the same time they pointed out that it is not possible at present to calculate the secondary effects of releasing these fish, due to interspecies predation among the fish stocks, and that this might alter the conclusion.

The working group on assessment of pelagic fish stocks in the Baltic (Anon. 1979b) used natural mortality coefficients for sprats ranging from 0.2 to 0.5 as input to the VPA when treating historic data. For prediction purposes they increased each value by 0.1 to account for predation by an increased stock of cod. Similar precautions were taken for several herring stocks.

The working group on crangonid shrimps (Anon. 1979d) calculated fishing and predation mortalities for *Crangon crangon* on the continental North Sea coast and found predation the dominating source of mortality. The ICES Advisory Committee on Fishery Management (ACFM) concluded (Anon. 1979e) that management measures for adult shrimps would be ineffective.

Of particular interest is the discussion in the 1979 report of the North Sea roundfish working group (Anon. 1979c) which discussed at some length the need for multispecies assessment before recommending extensive effort reductions. The report quotes Sparre (1979) who investigated some consequences of accepting the yield per recruit model. When the commercial fish in cod food are treated in a yield per recruit assessment as though they were one species, decreasing the effort on cod and accordingly increasing the spawning stock led to losses to other fisheries for direct human consumption far exceeding the gain in the cod fishery. Sparre did not profess to believe these figures, but pointed out they were a consequence of accepting the yield per recruit method. This of course worried the working group, but did not penetrate into the Chairman's Summary nor the ACFM report.

At the statutory meeting in Warsaw in October 1979 ICES decided to establish an ad hoc working group to identify the data background necessary for multispecies assessment work and to design means to its achievement, but before venturing upon a general discussion of the future of multispecies assessment in ICES it may be profitable to analyze in more detail the North Sea cod stock and its influence upon other fish stocks, using the Andersen and Ursin (1977) model.

Single Species and Multispecies Assessment for North Sea Cod

The yield and biomass curves for North Sea cod as estimated in the 1978 report of the North Sea roundfish working group (Anon. 1978) are shown in Fig. 1A with a few amendments. The ordinates are changed from yield per recruit and biomass per recruit to total yield and biomass.

The biomass curve, originally showing only spawning biomass, was raised by a constant (65 000 t) to account for immature biomass also. According to this assessment (which in its original form is the one discussed by Sparre (1979) and by the working group in its 1979 report), maximum yield would be achieved by reducing effort (i.e. F) to 30% of the 1977 value. Yield would increase by 43% (from 180 000 to 257 000 t) and biomass by almost a factor of 6 (from 0.22 to 1.27 Mt).

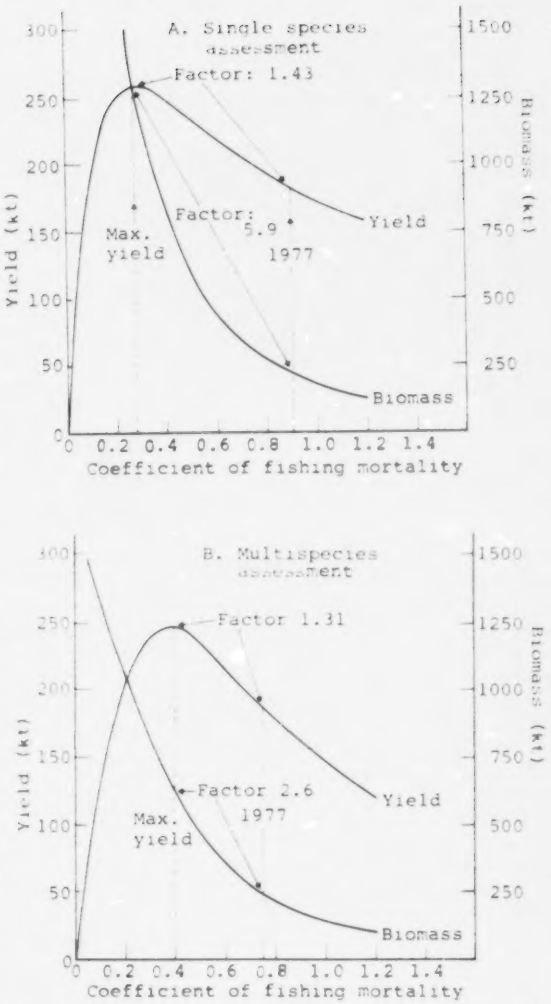

FIG. 1. Single species (A) and multispecies (B) stock and yield assessment for North Sea cod. The models used are Beverton and Holt (1957, redrawn from Anon. 1978) and Andersen and Ursin (1977).

Figure 1B shows similar curves from a multispecies assessment with the Andersen and Ursin (1977) model in an application described in Chapter 6 of the 1977 paper, but with amendments and corrections specified by Ursin (1978) and after incorporation of recent catch data from various 1979 working group reports. The calculations begin on Jan. 1, 1975, and are carried through 11 yr until the end of December 1985. For the years 1975–77 actual estimates of fishing mortalities and recruitment were used for the 11 fish species included. For the years 1978–85 estimates of F and average recruitment were those of 1977. Exceptions are herring and Norway pout, for which effort reductions after 1977 were

assumed. The estimated F of adult herring was about 1.5 in 1975–77. For 1978–80, when fishing for herring was not allowed, F was reduced to 0.1, with an increase to 0.2 in 1981, anticipating a decision to begin a modest fishery after some rebuilding of the depleted stock. For Norway pout an F value of 0.82 had been estimated for 1975–76. Reductions to 75 and 60% were assumed for 1977 and 1978–85, respectively, because an area in the northwestern North Sea became closed to small-meshed fisheries. The only variable during the calculations was the F value for adult cod (F(cod)) which took on values ranging from 0.05 to 1.20, always using the same value through the 11 yr. Among the values used was 0.75, which was estimated for 1977. Plotting cod yields in 1985 and biomasses at the end of 1985 as done in Fig. 1B for a range of values of F(cod) does not quite give steady values comparable to the single species assessment of Fig. 1A, but the differences between 1984 and 1985 were small enough to be neglected, and the 1985 values may be treated as steady-state values.

The yield and biomass curves are of course fairly similar in the single species and multispecies cases, but there are important differences. The biomasses at low F(cod) values are smaller in the multispecies model because of increased cannibalism among cod. Assuming constant recruitment of very young cod and of other species too, the fraction of cod in cod stomachs remains the same, but there are more cod and therefore cannibalism increases and recruitment to size-classes too big to be consumed is reduced. Reducing F(cod) to 30% of the 1977 value increases the biomass by a factor of 4.5 as compared with 5.9 in the single species case. Maximum yield is achieved with 53% of present effort (against 30%), another consequence of cannibalism. The result is that a reduction of F(cod) until maximum yield is achieved implies a biomass increase from 240 000 t to only 616 000 t, a factor of 2.6 instead of 5.9. The effect upon prey species is, therefore, likely to be less than found by Sparre (1979) when accepting the single species biomass assessment.

Another difference between the two assessments is that with the multispecies model there is a steeper yield decrease for high F(cod) values. This is due to recruitment overfishing which is introduced in the model by assuming that recruitment of cod can be described by the same type of empirical function which realistically describes the drop in herring recruitment in the North Sea in recent years (Andersen and Ursin 1977, Appendix). The parameter determining the slope of the stock–recruitment curve was tentatively given the same value for cod as for herring. The spawning stock of cod is calculated to be 30 000 t for F(cod) = 1.20 and it seems a sensible precaution to assume recruitment overfishing at this low population level.

The levels of yield and biomass curves in Fig. 1A and 1B depend on the assumptions on average recruitment made in the two cases. For details on the stock–recruitment function in the multispecies model, see Andersen and Ursin (1977), but a few general remarks are required here. The actual recruitment depends on density-dependent mortality of larvae and on predation mortality including cannibalism. Observed year-class strengths are introduced by adjusting a "carrying capacity" parameter, $\hat{R}_i$, for each species to a different value each year because the model cannot predict the observed variation in year-class strength whose causes remain obscure. The problem arises how to estimate an average value of $\hat{R}_i$ for each species for prediction purposes. This is the same problem as when ICES working groups must decide on an average recruitment to obtain forecasts by means of virtual population analysis. The arithmetic means of $\hat{R}_i$ estimates for 1966–75 were used. The effect of adopting this method is discussed by Ursin (1978).

Impact of North Sea Cod Upon Other Species

When the cod stock is increased in the multispecies model the larger of the other species tend to lose biomass and the smaller ones to gain. The discussion can therefore be simplified by pooling the species in two groups as follows.

Large species:
- Saithe (American pollock) (*Gadus virens*)
- Haddock (*Melanogrammus aeglefinus*)
- Whiting (*Merlangius merlangus*)
- Plaice (*Pleuronectes platessa*)
- Mackerel (*Scomber scombrus*)

Small species:
- Norway pout (*Trisopterus esmarki*)
- Dab and long rough dab (*Limanda limanda* and *Hippoglossoides platessoides*)
- Herring (*Clupea harengus*)
- Sprat (*Sprattus sprattus*)
- Sand eels (American sand lance) (*Ammodytes* sp.)

Figure 2 shows the response of yields and biomasses to changes in the cod fishery. Total yield and total fish biomass remain remarkably stable, but biomass and yield of large species are reduced when the cod stock increases at low F(cod) values. This is an effect of changes in the age structure of the cod population more than a direct effect of cod biomass. Reducing F(cod) means to leave the cod to live longer and grow bigger. Figure 3 (data from Daan 1975) shows the influence of cod size upon fish consumption by cod. Daan distinguished between commercial and noncommercial fish species. Commercial ones are mackerel, cod, whiting, haddock, herring, plaice, and sole. This group corresponds fairly well to "big species" of Fig. 2. Herring is placed differently, but Daan's investigation was carried out when there was still a sizable herring stock in the North Sea. Herring were older and bigger and therefore may actually have merited grouping with the larger species rather than with smaller ones. Daan's results show that not only does the fraction of fish in cod food increase with the size of cod, but also the fraction of commercial (big) species. Cod in the multispecies model therefore seem to behave like real cod, changing their diet as they grow.

By reducing F(cod) from the 1977 level of 0.75 to the value of 0.40 to give maximum yield of cod would influence the yield (in units of kilotonnes) of all 11 species as follows:

Yield	F(cod) = 0.75	F(cod) = 0.40	Difference
Cod	188	247	+59
Large species	847	646	−201
Small species	1368	1513	+145
Total	2403	2406	+3

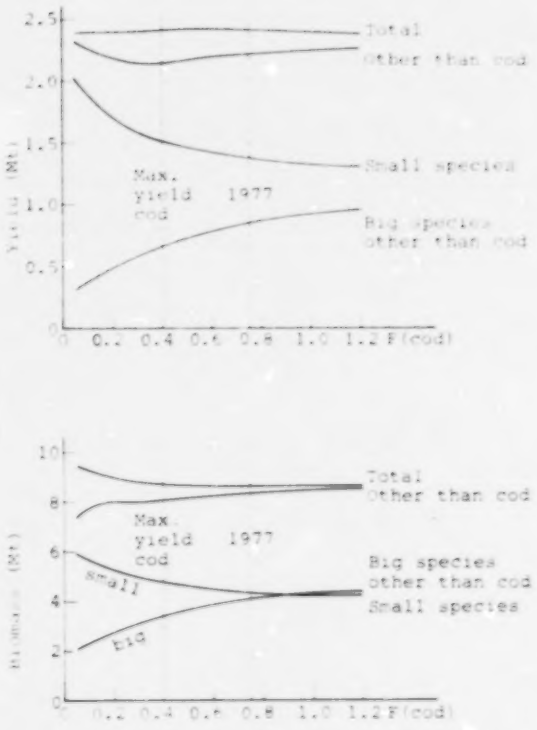

FIG. 2. Multispecies assessment of the response of yields and biomasses to changes in fishing effort upon cod.

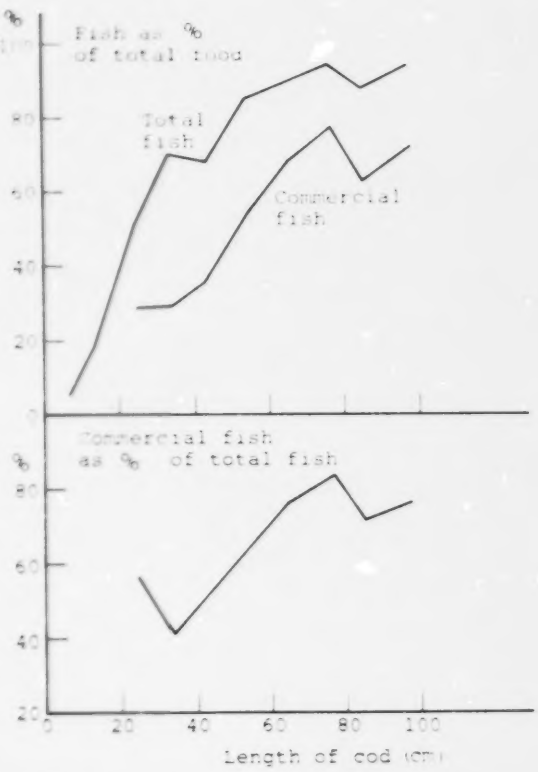

FIG. 3. Influence of cod size upon food composition. Data from Daan (1975).

It seems that the argument carried by Sparre (1979) and by the roundfish working group quoting him (Anon. 1979c) holds for big species only, or in practice, mainly for fish caught for direct human consumption. The fisheries for industrial purposes (meal, oil, fodder) behave differently.

The difference between the reactions of smaller fish and big fish to changes in cod biomass and age structure is reflected in the coefficients of predation mortality. For whiting, for instance, we find the following coefficients:

Whiting age-group	F(cod) = 0.75	F(cod) = 0.40	Difference
0	1.13	1.10	−0.03
1	0.62	0.67	+0.05
2	0.29	0.39	+0.10
3	0.14	0.23	+0.09
4	0.09	0.16	+0.07
5+	0.06	0.12	+0.06

Transferring predation pressure from 0-group whiting to the older age-groups, an increased stock of old cod utilizes the whiting stock better. As a secondary effect of reducing the stock of old whiting, cod ease the predation pressure upon 0-group whiting and upon all ages of the smallest species. In a sense, cod produce some of the extra fish biomass they consume. To analyze this effect the total fish production was calculated by numerical integration of numbers times body weight increments. In units of kilotonnes we have:

	F(cod) = 0.75	F(cod) = 0.40	Difference
Total fish production	8694	8995	301
Fish consumption by cod	464	1025	561
Surplus consumption by cod			260

Cod "produced" more than half their extra food requirements. It is probably an important mechanism in the marine ecosystem that a predator produces some of its own food by consuming competing predators.

Another example is the response of haddock food to an increased haddock stock in the North Sea. Jones (1979) found only a slight reduction in growth rate with a sevenfold increase in demersal haddock biomass although there was no evidence of surplus food awaiting exploitation when haddock biomass was low. A simple explanation with reference to the exercise above is that among the benthic invertebrates consumed by haddock there are some preying upon the same

species as haddock although mostly, perhaps, upon younger stages. Every time a haddock consumes one such predator it can continue eating the potential food of the consumed predator. This is in accordance with Steele's (1973) production budget for the North Sea in which only 1.4 g of benthos carbon m^2 is fish food out of 5.4 g produced. The rest is devoured by benthic carnivores.

We may conclude that information on food consumption by predator populations based on stomach analyses cannot be used directly to calculate losses to the fishery due to predation. The prey or some of it might not have been there to be consumed without the contemporary biomass and age structure of predator populations. Only a careful analysis of the food web reveals the effects of increasing or decreasing predator stocks. With this in mind the discussion of multispecies assessment in ICES can be resumed.

Future Multispecies Assessment in ICES

The intention of most fish stock management measures proposed by ICES and advanced by international bodies taking advice from ICES is to secure the maximum sustainable yield, or something close to it, of each stock separately. This goal becomes illusory to the extent that yields of predator stocks and of prey stoocks cannot be maximized at the same time, and, indeed, the exercise performed above indicates that drastic changes of predation patterns entrain management problems. Also, the accumulating information on really large quantities of fish being consumed by marine animals cannot be left unconsidered although such information is likely to overestimate the influence of predation as pointed out in the section on multispecies models.

The recent (October 1979) establishment of an ad hoc ICES working group to consider the data requirement for multispecies assessment may be an important step. For the model of this paper its terms of reference can to a large extent be interpreted as to find out what is needed to estimate the coefficients of vulnerability to predation (elements of the G array described) and to test the realism of this array by stomach investigations. Another urgent problem is the digestion rate which must be known so that measurements of stomach contents can be converted to food consumption.

The G array is practically identical in several models so that the final choice of model can be postponed. However, there will be little if any instigation to take advice to begin such work on a reasonable scale if the results cannot currently be utilized for assessment purposes even if such assessments are only tentative. The choice of model is therefore already important.

The Andersen and Ursin model has been in working order for multispecies assessment in the North Sea for some time (Ursin 1977, 1978), but is tedious to handle in the present form. It would be a time consuming task to implement a similar application in other areas. Simplifications could be made by starting over again with the "reduced model for rapid computation" (Andersen and Ursin 1977) and adding to it only what seems imminently necessary. The cohort analysis models (Pope 1979b; Helgason and Gislason 1979) are probably easier to handle (particularly Pope's). The latter may need a few amendments, but would remain charmingly simple. It should not be overlooked that prerequisite to introducing a new assessment method into ICES working groups is the need for a large number of people to understand the method to be used.

The best approach seems to be to instigate a Pope assessment scheme in most ICES areas. A first approach can be made quickly because the basic material remains the catch at age data already used. The array of values G_{ij} of vulnerabilities of prey j to predation by predator i could in the first place be developed as done by Pope in an extremely simple procedure. This will not be satisfactory, but one important task of an area based multispecies working group would be the continuous improvement of the elements of the G array for the area.

The North Sea presents a special problem because assessments are made by many working groups and because all three G-array models have already been, or are being, implemented there. Continued exercises with these models in a special working group might disclose the weak points of each and, particularly, whether the simplifying assumptions in Pope's model are actually too crude. This could produce valuable advice to other area working groups whose own modeling work could then be kept at a minimum if so desired. Their main multispecies effort would be the current acquisition of biological information to invest in the G array of vulnerability coefficients for their respective areas.

Single species assessment work would continue because of the importance of disclosing the extent to which multispecies and single species results differ and to solve problems with no obvious bearing upon species interaction.

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Species Interactions in the North Sea

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JONES, R. 1982. Species interactions in the North Sea, p. 48–63. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

This paper is concerned with calculations of energy flow through the North Sea ecosystem, and the implications of these calculations. The calculations are subject to the constraint that it ought to be possible to relate estimates of fish food requirements to other, and independent, estimates of secondary production in a way that seems biologically plausible. This was done without having to make any unreasonable assumptions. Estimates were also made of probable values of "transfer efficiencies" between trophic levels, and of how large virgin stocks of commercially exploited fish might have been.

Key words: ecosystem, North Sea, transfer efficiency, herbivore, primary production.

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On trouvera dans l'article qui suit un exposé des calculs du flux énergétique dans l'écosystème de la mer du Nord et de leurs implications. Pour ces calculs, il faut pouvoir établir la relation entre les estimations des besoins alimentaires des poissons, d'une part, et d'autres estimations, indépendantes celles-là, de la production secondaire, d'autre part, d'une manière biologiquement plausible. On y est arrivé sans avoir recours à des suppositions déraisonnables. Nous avons en outre estimé les valeurs probables d'« efficacités de transfert » entre les niveaux trophiques et de l'importance qu'ont pu avoir des stocks vierges de poissons exploités commercialement.

Introduction

The objectives of this study were as follows: (1) to use a simple framework for examining trophic interactions and hence to try to satisfy the food requirements of the major fish species in the North Sea given estimates of the potential food available; (2) to do this for periods at the beginning and end of the 1960s when the ratios of pelagic to demersal fish biomass were very different; (3) to consider how much larger fish stocks could have been under virgin stock conditions; (4) to consider the probable food requirements of larval and juvenile fish; (5) to consider how much of the herbivore production is taken up by fish, including the larval and juvenile stages; and (6) to estimate probable values for the transfer efficiencies through various trophic levels.

A Simple Framework for Examining Trophic Interactions (Fig. 1)

The first objective is to compare the food requirements of the principle fish species with the food available, and to see how closely they can be matched up. To do this, it is first necessary to decide on convenient groupings of the various species, and to identify the principle energy pathways between them. The arrangement that was finally adopted for this study is shown in Fig. 1.

Ecological considerations suggest that the larger individuals of the principal exploited fish species should be divided into at least two groups. These are (1) "adult" herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) (group P) and (2) "adults" of the larger species of demersal fish species (group D). In this context the word "adult" is used to refer, loosely, to the larger or mainly mature-sized individuals. Species included in group D for which stock assessment data are available are cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), saithe (*Pollachius virens*), plaice (*Pleuronectes platessa*), and sole (*Solea solea*).

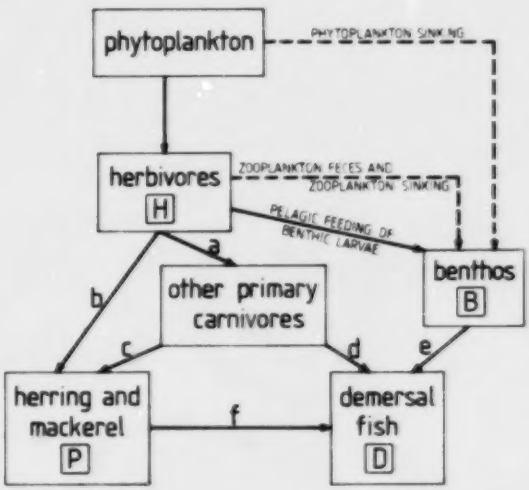

FIG. 1. Diagrammatic representation of the principal energy flows to the fish species.

Figure 1 shows the principal energy pathways by which adult pelagic and demersal fish are linked to the two principle energy sources which are (1) herbivores (group H) and (2) the benthos (group B). Also included in the figure is a species

TABLE 1. Adult stock sizes of major fish species in the North Sea (from Jones and Richards 1976).

Species	Biomass of stock (kt)		Age (yr)	M[b]
	Early 1960s (period)	Late 1960s (period)		
Herring (*Clupea harengus*)	2100 (1959–61)	799 (1968–70)	2–8	0.1
Mackerel (*Scomber scombrus*)[a]	3000 (early 1960)	950 (1968–70)	3–7	—
Cod (*Gadus morhua*)	192 (1963)	367 (1968–70)	2–12	0.2
Haddock (*Melanogrammus aeglefinus*)	118 (1959–61)	597 (1968–70)	2–8	0.2
Norway pout (*Trisopterus esmarkii*)	169 (1961–63)	415 (1968–70)	1–3	0.7
Whiting (*Merlangius merlangus*)	102 (1959–61)	217 (1968–70)	2–8	0.2
Saithe (*Pollachius virens*)	193 (1960–62)	896 (1968–70)	2–14	0.2
Plaice (*Pleuronectes platessa*)	390 (1959–61)	471 (1968–70)	2–20	0.1–0.25[c]
Sole (*Solea solea*)	130 (1959–61)	87 (1968–70)	2–14	0.1

[a]Mackerel stock sizes from Anon. (1974) and Hamre (1978).
[b]Values of M (instantaneous coefficient of natural mortality) adopted for determining stock size.
[c]Values of M taken at 0.25 and 0.20 for 2 yr-old males and females and 0.15 and 0.10 for older males and females, respectively.

TABLE 2. Annual food requirement of various fish species (kcal·m^{-2}·yr^{-1})[a] (from Jones and Richards 1976).

Group	Species	1959–1961	1968–1970	Change
Pelagic group (P)	Herring	19.0	8.1	
	Mackerel	27.1	8.6	
	Total	46.1	16.7	−29.4
Demersal group (D)	Cod	1.3	2.4	
	Haddock	0.8	4.0	
	Whiting	0.7	1.4	
	Saithe	1.2	6.0	
	Plaice	2.6	3.1	
	Sole	0.8	0.6	
	Other species[b]	4.4	3.5	
	Total	11.8	21.0	+9.2

[a]Conversion factors from grams wet weight to kilocalories: for herring and mackerel, 1.36 kcal·g^{-1} wet weight of fish; for sprats, sand eels, and Norway pout combined, 1.1 kcal·g^{-1} wet weight; for all other species, 1.0 kcal·g^{-1} wet weight (Jones and Hislop 1978).
[b]Excluding Norway pout, sand eels, and sprats. Conversion to square metres adopting 0.57×10^{12} m^2 for the area of the North Sea.

grouping referred to as "other primary carnivores." This group contains all individuals other than those in group P that feed on herbivores. It includes the larvae and pelagic juveniles of the fish species in groups P and D, all life stages of smaller fish species such as sand eels (*Ammodytes* spp.), sprats (*Sprattus sprattus*), and Norway pout (*Trisopterus esmarkii*) that might serve for food for the larger fish groups P and D, and also all those invertebrates that feed on herbivores.

The diagram is arranged to show that adult herring and mackerel derive their food partly by eating herbivores and partly by eating "other primary carnivores." "Adult" demersal fish derive food from three sources, i.e. from the benthos, from "other primary carnivores," and from group P.

Changes in Relative Abundance of Demersal and Pelagic Fish

During the 1960s there was a decline in the biomass of herring and mackerel and an increase in the biomass of various other species, particularly the gadoids. This has been discussed in particular by Cushing (1980), and several workers (e.g. Andersen et al. 1973; Lett et al. 1975) have pointed out how, in general, within a closed ecosystem changes in the biomass of any one major group will be expected to influence the biomass of other species or groups.

From a consideration of Fig. 1 it is easy to see how a reduction in the stocks of adult herring and mackerel might have permitted more food to have become available for adult demersal fish. For example, a reduction in flow *b* could have been associated with an increase in flow *a* and, hence, indirectly with an increase in flow *d*. Similarly a decrease in flow *c* could have been directly associated with an increase in flow *d*.

Given estimates of biomass, it should be possible to determine how the reduction in food eaten by adult herring and mackerel compared with the increased food needed by adult demersal fish.

Estimates of the food requirements of the "adults" of the major fish species can be determined from estimates of the biomass for each of the major stocks. Estimates of stock biomass based on data given in various ICES Fish Stock Working Groups are shown in Table 1, taken from Jones and Richards (1976).

To a first approximation, annual food consumption can be obtained by multiplying the stock biomass (in kilocalories (1 cal = 4.19 J)) by an appropriate factor. For gadoids, values estimated by Jones and Richards (1976) suggest that annual food consumption would be between three and four times the biomass. Other authors (e.g. Mann 1965) have used a factor of up to 10, but this was for much smaller fish (freshwater species in the River Thames) that were growing faster (relative to their size) and living at higher temperatures. In this study, conversion factors of 3–4 have been used. Calculations based on simulations of the life history using equations (1) and (7) in Appendix 3, as modified for adults in section 2 of that Appendix, give similar results. All values were converted to kcal·m^{-2}·yr^{-1} by adopting a value of 0.57×10^{12} m^2 for the area of the North Sea.

Table 2 shows the annual food requirements of the major fish species taken from Jones and Richards (1976). For adult herring and mackerel (group P) the estimates of food require-

ments are the following: 1959–61, 46.1 kcal·m $^{-2}$·yr $^{-1}$; 1968–70, 16.7 kcal·m $^{-2}$·yr $^{-1}$. During the 1960s, therefore, the food requirements of this group declined by −29 kcal·m $^{-2}$·yr $^{-1}$.

For the demersal fish (group D), estimates of annual food requirements for cod, haddock, whiting, saithe, plaice, and sole are given in Table 2.

In addition to the major pelagic and demersal species about 30 minor species are taken commercially. No estimates are available of their biomass but it is necessary to allow something for their food requirements. This can be done from a consideration of the landings of these species. In the period 1959–61, landings of minor and unidentified species made up about 250 000 t annually. The corresponding figure for the later period is about 200 000 t. If 1 g wet weight is regarded as equal to 1 kcal, these landings are equivalent to 0.439 and 0.351 kcal·m $^{-2}$, respectively.

If a production/food ratio of 0.20 is assumed (see later considerations on ecological efficiencies for exploited individuals), this would indicate, as conservative estimates, food requirements of about 2.19 and 1.76 kcal·m $^{-2}$·yr $^{-1}$. If it is further assumed that for these species the landings represent about half of the total production, the food requirements become 4.38 and 3.51 kcal·m $^{-2}$·yr $^{-1}$, respectively. Most minor species are taken demersally and as a first approximation, therefore, these values have been included in the food requirements of group D.

The results are included in Table 2, which show that the total values for the demersal fish group D are the following: 1959–61, 11.8 kcal·m $^{-2}$·yr $^{-1}$; 1968–70, 21.0 kcal·m $^{-2}$·yr $^{-1}$. Compared with a decline of 29 kcal·m $^{-2}$·yr $^{-1}$ for group P, the increased food consumption for group D amounts to only 9 kcal·m $^{-2}$·yr $^{-1}$. Norway pout, sand eels, and sprats are regarded as part of the "other primary carnivores" group and have been excluded from groups P and D.

These preliminary computations suggest that the decline in food requirements of adult herring and mackerel was greater than the increased food requirement of demersal fish.

A Comparison of Food Requirements and Food Available

Given estimates of the annual food requirement of groups P and D, and of the annual production levels of groups H and B, it should be possible to determine values for the various flows *a* through *f* (Fig. 1), and to do this for the beginning of the 1960s (1959–1961) and for the end of the 1960s (1968–1970).

Food for the various fish species is derived, directly or indirectly, from the production of pelagic herbivores (H) and from the production of benthos (B). Some individuals, such as the larger cod, may also feed on herring (flow *f* in Fig. 1).

For herbivores, Steele (1974) has estimated production in the North Sea as about 175 kcal·m $^{-2}$·yr $^{-1}$. A very similar value is used by Crisp (1975).

The production of benthos available as food for fish is more difficult to estimate. Steele (1974) estimated that the annual production of macrobenthos in the North Sea was about 20–50 kcal·m $^{-2}$. Other estimates are quite variable, but provide little reason for rejecting this range of values. Not all macrofauna production will be available as food for demersal fish, however, as some of it will be consumed by benthic carnivores. Some allowance must also be made for the food requirements of the demersal stages of the juveniles of the individuals in group D (see later). If average production is taken as 30 kcal·m $^{-2}$·yr $^{-1}$, this could suggest a production of food for the "adult" fish in group D of about 10 kcal·m $^{-2}$·yr $^{-1}$.

Included in the herbivores are those pelagic stages of benthic larvae that feed on phytoplankton. The settlement of these on the bottom diverts a certain amount of herbivore production to the benthos. According to A. Eleftheriou (Marine Laboratory, Aberdeen, personal communication) the percentage of herbivore production diverted in this manner is likely to be very small and for computational purposes just 1 kcal·m $^{-2}$·yr $^{-1}$ has been allowed for this.

From these considerations, the estimates of herbivore production (H) going to the pelagic food chain and of benthic production (B) going to group D become the following: for H, 174 kcal·m $^{-2}$·yr $^{-1}$; for B, 10 kcal·m $^{-2}$·yr $^{-1}$.

Comparison of the flows from H and B with the flows going to P and D suggests that it should be possible to relate food requirements to food available without having to make any unrealistic assumptions. For the demersal fish during the period 1959–61, B provides 10 and D needs 12 units, suggesting that about 80% of the demersal fish food could have come from the benthos.

For the later period, if it is assumed that the production of B is unchanged, it is necessary to suppose that the increased demersal fish food requirements came via "other primary carnivores." This is not necessarily unreasonable if it is noted that (1) a major increase in the demersal group was due to saithe, a species that derives its food from the "other primary carnivores" group, and (2) of the remaining species, the greatest increase was in the biomass of haddock. Although normally a benthic feeder, analysis of stomach contents shows that in 1968, when haddock biomass was close to an all time maximum, more than 85% of the food consisted of sand eels (Jones and Richards 1976).

Overall the reduction in the food requirements of herring and mackerel amounted to 29 kcal·m $^{-2}$·yr $^{-1}$ whereas the increase in the food requirements of the demersal food group was only 9 kcal·m $^{-2}$·yr $^{-1}$. To satisfy the increase of 9 units, in terms of the decrease of 29 units, it is necessary to make some assumptions about the proportion of herring and mackerel food coming from "other primary carnivores." For example, there would be a difficulty in relating the value of 9 to the value 29 if herring and mackerel fed exclusively on herbivores so that all of their food came via flow *b* (Fig. 1). A reduction in flow *b* would have to be diverted to group D via the "other primary carnivores" group. To yield an extra 9 units to group D would require a 31% transfer efficiency through the "other primary carnivores," which seems unlikely. Conveniently, the food of herring to a certain extent, and of mackerel to a greater extent, comes partly from the "other primary carnivores" group via flow *c*. Figure 1 shows that a reduction in flow *c* could theoretically permit an equivalent increase in flow *d*. Calculations below show that the necessary increase of 9 kcal·m $^{-2}$·yr $^{-1}$ for demersal fish can be accounted for in this way, without having to suppose that an

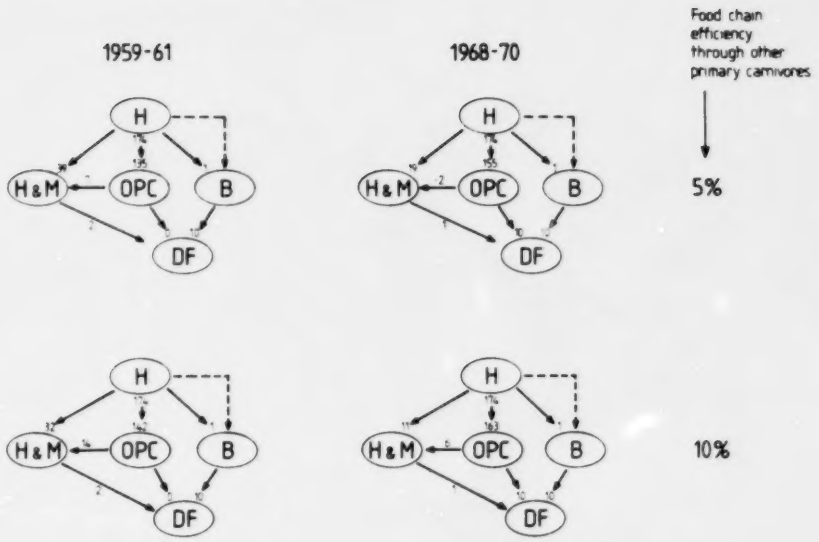

FIG. 2. Some possible sets of energy flows in the North Sea. H, herbivores; H & M, adult herring plus adult mackerel; B, benthos; DF, demersal fish; OPC, other primary carnivores. Numbers refer to annual flows in kcal·m^{-2}·yr^{-1}.

improbably large proportion of herring and mackerel food necessarily comes from "other primary carnivores."

Given estimates, or assumptions, about the transfer efficiencies[1] through "other primary carnivores" and through group P, it is a comparatively simple matter to estimate values for the flows *a* through *f* in Fig. 1. Theoretical details are given in Appendix 1, and results are shown in Table 3 and Fig. 2. Sets of flows are shown for each time period, and for values of the transfer efficiency through the "other primary carnivores" (ϵ_1) of 0.05 and 0.10 (see below). The transfer efficiency through group P (ϵ_2) to group D is assumed to be 0.04 (see below). Various observations can be made about these results. First, the proportion of "adult" herring and mackerel food coming from the "other primary carnivores" needs to be 15–30% at the beginning of the 1960s and −12–35% at the end of the 1960s. On average, these values appear not unreasonable as herring have been known to eat sand eels in considerable quantities (Hardy 1924) and mackerel frequently eat small fish (Walsh and Rankine 1979). Second, only 6–22% of the secondary production goes directly to group P, whereas the remainder has to pass through at least one trophic stage before it becomes available to group D. This has important implications for the relative fish yields from these two groups. Third, in certain years, and probably in certain seasons of the year, "adult" demersal fish can derive as much of their food from the pelagic food chain as from the benthic food chain. Fourth, a proportion of the food for demersal fish may come from group P (i.e. flow *f* in Fig. 1). This may be important for particular species at particular times (e.g. cod feeding on herring (Daan 1973, 1975; Sparre 1979)).

These computations suggest that the food requirements of the main commercial species can be accounted for, both at the

TABLE 3. Some possible sets of energy flows (reference Fig. 2).

	1959–61		1968–70	
Inputs				
ϵ_1[a]	0.05	0.10	0.05	0.10
ϵ_2[b]	0.04		0.04	
H	174		174	
B	10		10	
P	46		17	
D	12		21	
Outputs[c]				
a	135	142	155	163
b	39	32	19	11
c	7	14	−2	6
d	0	0	10	10
e	10	10	10	10
f	2	2	1	1
100 *c*/P[d]	15	30	−12	35

[a]Transfer efficiency through the "other primary carnivore" group (see text).

[b]Transfer efficiency from group P to group D (see text).

[c]Calculated using equations (6)–(10) in Appendix 1.

[d]Percentage of herring and mackerel food coming from "other primary carnivores."

[1]Transfer efficiency through group X going to group Y = (energy flow from group X to group Y)/(energy entering group X). Note that this is not necessarily the same as either "ecological efficiency" or "food chain efficiency" as defined by Slobodkin (1961).

beginning and at the end of the 1960s, without having to make any unreasonable biological assumptions.

Further Computations

To a first approximation, the considerations above suggest that the increased demersal fish food requirements at the end of the 1960s could have been provided via the pelagic food chain. In this section, the objective is to extend these calculations to determine (1) what possible upper limits to the stocks of herring, mackerel, and demersal fish might be set within the framework shown in Fig. 1, (2) the likely food requirements of larval and juvenile fish, (3) what proportion of the "other primary carnivores" is likely to consist of fish, and (4) probable values for the various transfer efficiencies.

Upper Limit to the Biomass of Fish

It is useful to extend these calculations to consider the food requirements of the commercially more important fish species under virgin stock conditions.

For example, Assessment Working Groups frequently base their calculations on the assumption that natural mortality (M) and recruitment remain constant when fishing effort changes. For herring, for example, assessments are usually based on a value of $M = 0.1$. Calculations using this value suggest that in the absence of exploitation, the food requirements of the North Sea herring stock should have been about 5.7 times that at the beginning of the 1960s and 12 times that at the end of the 1960s. This leads to estimates, using values in Table 2, of $19 \times 5.7 = 108$ kcal·m^{-2}·yr^{-1}, or $8 \times 12 = 96$ kcal·m^{-2}·yr^{-1}.

If it is assumed that the virgin mackerel stock was no higher than it was at the beginning of the 1960s, 27 kcal·m^{-2}·yr^{-1} can be allowed for mackerel food. This leads to a conservative estimate of about 130 kcal·m^{-2}·yr^{-1} for the food requirements of group P.

From adult demersal fish, a value of $M = 0.2$ is usually adopted by Assessment Working Groups. Calculations suggest that in the absence of exploitation, food requirements could increase by a factor of about 4–5. If this is applied to the more conservative 1960s food requirement (i.e. 7.4 kcal·m^{-2}·yr^{-1} in Table 2) this leads to a value of 33 kcal·m^{-2}·yr^{-1}. If an allowance of 5–6 kcal is added for "other species," plus another 5–6 for demersal juveniles, this leads to a conservative estimate for group D of about 44 kcal·m^{-2}·yr^{-1}.

For P and D combined, the food requirements are therefore 174 kcal·m^{-2}·yr^{-1}, which is just about equal to the value of food available (i.e. H + B = 184 kcal·m^{-2}). This leaves no room for "other primary carnivores" at all. There does not appear to be any way out of this difficulty by attempting to increase the amount of available food. Thus, it is difficult to see how herbivore production could be significantly increased without increasing the particular primary production, which is believed to be about 900 kcal·m^{-2}·yr^{-1} (Steele 1974). If all of this is consumed by herbivores, and about two-thirds is assimilated, the assimilated food for herbivores would be 600 kcal·m^{-2}·yr^{-1}. Herbivore production of 175 kcal·m^{-2}·yr^{-1} therefore implies a net transfer efficiency of 29%. To increase herbivore production would therefore require a significant increase in herbivore transfer efficiency and/or in particulate production. Neither of these seem to be likely possibilities.

The particulate energy input to the benthos would have to come partly from the 300 kcal·m^{-2}·yr^{-1} of nonassimilated herbivore food released as feces (Steele 1974; Davies 1975). Before this becomes available to the benthic fauna, however, it is believed that a bacterial stage is involved (Fenchel and Jørgensen 1977; Gerlach 1978; Paerl 1978). Steele (1974) has pointed out the difficulty of fitting in a bacterial stage, and also of finding enough energy to account for meiobenthos production as well as for macrobenthic production of 20–50 kcal·m^{-2}·yr^{-1}. There would, therefore, appear to be little scope for increasing macrobenthic production in this way.

In addition to primary particulate production, a further 20% of primary production may occur in the form of dissolved organic carbon (Parsons and Seki 1970). This, however, can probably all be accounted for if one tries to account for the respiration of bacteria in the water column and in the sediment. By taking account of the soluble organic production it may be possible to account for the overall energy demands of the detritus food chain (Fenchel and Jørgensen 1977; Larsson and Hagstrom 1979). There would be little scope for increasing the production of macrobenthos, however.

Additional energy for demersal fish could be provided by adopting a transfer energy through "other primary carnivores" greater than 5–10%. Later considerations, however (see next section), suggest that higher transfer efficiencies are more likely to be associated with the production of small individuals, such as fish larvae, than with the production of the larger individuals needed as food for groups P and D. Higher transfer efficiencies can more easily be justified for accounting for the food requirements of invertebrate secondary carnivores than for the food requirements of groups P and D.

There does not appear to be much scope therefore for finding the food necessary for supporting biomasses of the commercially important fish species, as large as five times present-day levels.

Food Requirements of Larval and Juvenile Fish

Part of the "other primary carnivore" group consists of fish, including larval and juvenile fish. It is relevant, therefore, to try to determine the fish component of this group. The food requirements of larval and juvenile fish can be determined if something is known about the numbers at age throughout the larval and juvenile stages. For most marine species, little is known about this part of the life history, except that mortality rates must be much higher than they are in the adult stage. One approach to this problem is to consider ways in which biomass might change with age, as changes in biomass during the first 1 or 2 yr are likely to be very much smaller than changes in numbers. The basis of this approach is illustrated in Fig. 3a. This represents one possible relationship between biomass and age for North Sea haddock under steady-state conditions and present-day levels of exploitation.

Haddock mature at 2 yr of age and at body weight of about

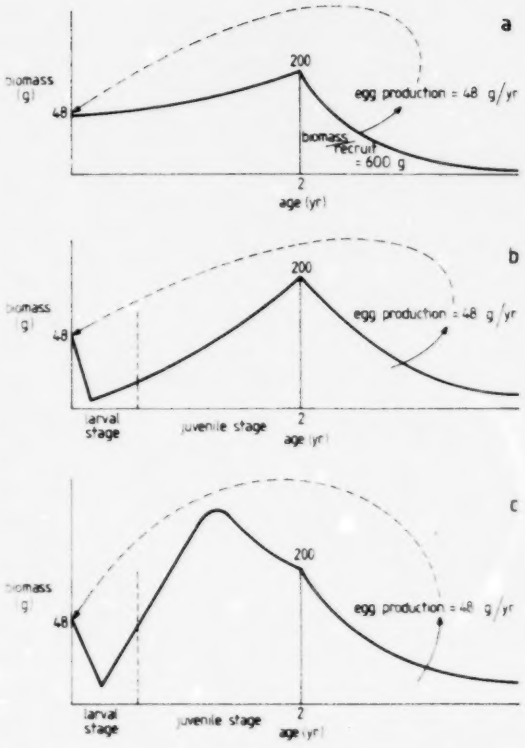

FIG. 3. Some possible relationships between biomass and age prior to maturity

200 g. Under steady-state conditions, calculations using the Beverton and Holt equations (Beverton and Holt 1957) show that the biomass per recruit would be about 600 g. Estimates of egg production per recruit indicate that the egg production would be about 16% of the female biomass or, to first approximation, about 8% of the total mature biomass (Appendix 2). Egg production should therefore amount to 48 g·yr^{-1}.

Under steady-state conditions, 48 g·yr^{-1} also represents the biomass of individuals at zero age. During the first 2 yr of life, the biomass of a cohort should, therefore, increase by a factor of about 4. If an assumption is made about the rate of change of biomass throughout the first 2 yr it is possible to estimate the biomass at age throughout the whole of the larval and juvenile period. One possibility is to assume a simple exponential relationship to relate the biomass at zero age to that at 2 yr of age.

Once biomass at age for the first 2 yr has been determined, as in Fig. 3a, it is a comparatively simple matter, given a weight at age relationship, to determine numbers at age. For the first 2 yr, estimates of the food required to satisfy a growing cohort can then be determined without difficulty. Theoretical details are given in Appendix 3. Estimates of the food required by larval, juvenile, and adult stages of haddock, herring, and sand eels are given in Appendix Tables A1 and A2. These data have been combined in various ways in subsequent calculations for determining the likely range of food requirements for larval and juvenile fish.

A further consideration is that there might be mortality of eggs and larvae prior to, and at first feeding, so that the weight of very young larvae may be less than the weight of eggs produced by the mature stock. This possibility is illustrated in Fig. 3b. To take account of this, the calculations have been done for various assumptions about initial mortality; altogether, five options have been considered. Assuming current rates of exploitation for mature fish: A, assuming 90% egg and initial first feeding mortality; B, assuming 50% egg and initial first feeding mortality; C, assuming zero egg and initial first feeding mortality. Assuming mature individuals experience natural mortality only ($Z = 0.2$): D, assuming 90% egg and initial first feeding mortality; E, assuming 50% egg and initial first feeding mortality.

Yet another possibility is illustrated in Fig. 3c. This represents the situation in which a cohort reaches its maximum biomass at an earlier age than depicted in either Fig. 3a or 3b. The situation shown in Fig. 3a (corresponding to option C) leads to relatively high estimates of the food requirements of larvae and juveniles. The option shown in Fig. 3c could lead to even larger estimates of juvenile food requirements.

Calculations based on the alternative options A through E have been used to determine the food requirements of the fish component of the "other primary carnivores" group. To do this it is necessary to consider how the various life history stages fit into the food web in Fig. 1.

Figure 4 helps to illustrate some of the important considerations. Figure 4a represents the various life history stages for a single species (i.e. larvae, juveniles, and adults). The individuals in each of the three stages consume foods F_1, F_2, and F_3, respectively. These foods do not necessarily consist of the same prey species and may not even come from the same trophic level. The deaths of larvae, juveniles, and adults lead to the productions P_1, P_2, and P_3, respectively.

The problem is to consider which of the F values represent energy inputs to "other primary carnivores" and which of the P values represent outputs. For example, for species such as sand eels, Norway pout, and sprats, all three life history stages are included within the "other primary carnivores" group. The simplest assumption is that for these species energy input is equivalent to $F_1 + F_2 + F_3$ while total production is equivalent to $P_1 + P_2 + P_3$. This assumes, however, that the larval stages are consumed by animals outside the "other primary carnivores" group. Although this may happen to some extent, a more realistic assumption is that larvae are so small that they are mainly eaten by animals such as juvenile fish, small fish, and invertebrate carnivores within the "other primary carnivores" group.

The scheme illustrated in Fig. 4b may therefore be a more realistic approximation, i.e. larval production is shown as food for juveniles (in practice not necessarily of the same species). Net food requirements are therefore $F_1 + F_2 + F_3 - P_1$ and net production to higher trophic groups is $P_2 + P_3$.

For herring and mackerel (Fig. 4c) only the larval and juvenile stages are represented in the "other primary carnivores" group. For these, the net food requirements are equivalent to $F_1 + F_2 - P_1$ and the net production to P_2. For

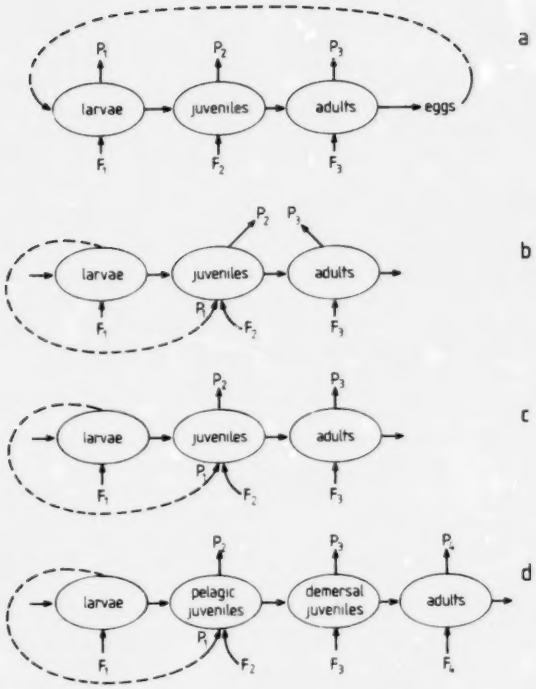

FIG. 4. Considerations of "ecological efficiency."

species in group D (Fig. 4d) juveniles are represented as pelagic juveniles and demersal juveniles. To allow for the "other primary carnivores" component of these species, net food is equivalent to $F_1 + F_2 - P_1$ and net production to P_2. The food requirement of the demersal juveniles (i.e. F_3 in Fig. 4d) has to be added to F_4 to arrive at the total food requirements for group D individuals.

Finally, Table 4 summarizes data from Appendix Tables A1 and A2 in a form suitable for estimating the food requirements of the fish component of the "other primary carnivores" group. For haddock and herring the food requirements are expressed as percentages of the food required by the adults.

For example, for larvae and juveniles, the values given are equal to $100(F_1 + F_2 - P_1)/F_4$, where F_4 is equivalent to F_3 in the case of herring (but F_4 in the case of haddock, Fig. 4d). For all given options, the values of F_4 for the present-day adult stock have been adopted. For sand eels the values for all stages are expressed as percentages of the food requirements of adults and juveniles, i.e. these are equivalent to $100(F_1 + F_2 + F_3 - P_1)/(F_2 + F_4)$.

Values of F_i are given in Appendix Tables A1 and A2. The results in Table 4, for example, show that the net food requirements of haddock larvae and pelagic juveniles could range from 16 to 257% of the food consumed by the currently exploited level of adult stock. The value of 16% applies to the present-day level of exploitations if there is a 90% mortality of eggs and first feeding larvae. At the other extreme, the value of 257% applies to the unexploited stock if there is 50% mortality of eggs and of first feeding larvae. In general, the food requirements of larvae and juveniles can be significant compared with the food required by present-day adults. The exact value, however, depends (1) on the mortality rates of eggs and first feeding larvae and (2) on the point in the life history where maximum biomass is reached. The values obtained above could, for example, be underestimates if biomass varies with age as depicted in Fig. 3c.

The values obtained in Table 4 can be used, in conjunction with the values in Table 2, to estimate the food requirements of larval and juvenile fish. The results of these computations are shown in Table 5 for each of the options A through C.

Demersal feeding of demersal fish juveniles amounts to 4–5 kcal·m^{-2}·yr^{-1} at the beginning of the 1960s and 7–9 kcal·m^{-2}·yr^{-1} at the end. These amounts have to come from the benthos in addition to the 10 kcal·m^{-2}·yr^{-1} assumed in Table 3 and Fig. 2.

The pelagic stages of the juveniles of demersal fish and other species require 2–9 kcal·m^{-2}·yr^{-1} at the beginning of the 1960s and 3–16 kcal·m^{-2}·yr^{-1} at the end.

To calculate the food requirements of sand eels, Norway pout, and sprats, an estimate is required of the combined biomass of these species. According to R. Bailey (Marine Laboratory, Aberdeen, personal communication) probable values for sand eels and sprats are the following: sand eels, 1.3 Mt; sprats, 1 Mt. For Norway pout the value is about 0.3 Mt (Table 1). The total is about 3 Mt. To convert to energy content, a factor of 1.1 has been adopted. Food consumption has been taken as four times biomass. This leads to an estimate of the food consumption of these three species combined of 23 kcal·m^{-2}·yr^{-1}.

It is not certain how large the biomass of sand eels and sprats was in 1959–61 compared with their biomass at the end of the 1960s. For computational purposes the same estimate has been used for both time periods, for all three species. If 23 kcal·m^{-2}·yr^{-1} is assumed to apply to both the juveniles and the adult stages, an allowance for the food requirements of all stages can be obtained using the values for sand eels shown in Table 4 (i.e. 107% for option A, 124% for option B, and 139% for option C). This leads to the estimates ranging from 25 to 32 kcal·m^{-2}·yr^{-1} for these three species shown in Table 5.

Combining values leads to estimates of food requirements of the various fish components of the "other primary carnivores" group. These range from 49 to 112 kcal·m^{-2}·yr^{-1} for the period 1959–61 and from 40 to 81 kcal·m^{-2}·yr^{-1} for the later period.

When the estimates obtained at the end of the previous section (Table 5) are compared with the estimates for flow *a* given in Table 3 it appears that the fish component of the primary carnivores group required about 35–80% of the food available in the period 1959–61. For the period 1968–70, the corresponding range was about 25–50%. If option C is rejected as the least likely of the three options A, B, and C, percentages nearer the lower ends of these ranges are to be preferred. These results tend to suggest that the fish component of the "other primary carnivores" group is unlikely to be much above 50%, and may easily be less than this. This is not inconsistent with the suggestion made by Steele (1965)

TABLE 4. Percentage food requirements of various stages of fish.

	Option[c]					Reference diagram
	A	B	C	D	E	
Haddock (larvae + pelagic juveniles)[a]	16	50	77	66	257	Fig. 4d
Haddock (demersal juveniles)[a]	32	39	45	43	64	Fig. 4d
Herring (early 1960s) (larvae + juveniles)[a]	47	101	154	64	15	Fig. 4c
Herring (late 1960s) (larvae + juveniles)[a]	73	143	205	—	—	Fig. 4c
Sand eels (all stages)[b]	107	124	139	—	—	Fig. 4b

[a]Food requirements as percentages of the food required by the present-day adult stock.
[b]Food requirement for all stages as percentages of food required by juveniles + adults.
[c]See footnote to Table 6.

TABLE 5. Summary of food requirements of North Sea fish species.

	1959–61			1968–70		
Group P						
Herring adults	19			8		
Mackerel adults	27			9		
	46			17		
Group D						
Demersal adults	7.4			17.5		
"Others"	4.4			3.5		
	[a]A	B	C	A	B	C
Demersal juveniles of demersal fish and others	4	5	5	7	8	9
Subtotal	16	17	17	28	29	30
Other primary carnivores						
Herring and mackerel (larvae and juveniles)	22	46	71	12	23	33
Pelagic stages of juveniles of demersal and "others"	2	5	9	3	9	16
Norway pout and sand eels and sprats (all stages)	25	28	32	25	28	32
Subtotal	49	79	112	40	60	81

[a]See footnote to Table 6.

that this proportion might be about 50%.

This conclusion is based on the assumptions about biomass and age depicted in Fig. 3b. If the alternative depicted in Fig. 3c is preferred, the food requirements of the young stages could be considerably higher than calculated above. Overall, the options appear to be that (1) the fish component of the "other primary carnivores" group is about 50% or (2) the fish component is considerably higher due to a relatively high demand for food by the young stages of the various fish species.

There is a decline in the fish component of the "other primary carnivores" group between the two periods. This may be an indication of an increase in invertebrate carnivores. Alternatively it could simply be a consequence of the assumption that there was no change in the stocks of Norway pout, sand eels, and sprats. For example, the fish proportions of the "other primary carnivores" group can be kept constant by allowing the combined biomass of Norway pout, sand eels, and sprats to increase by a factor of about 2 between the two periods.

It appears, therefore, that the fish component of the "other primary carnivores" group could account for at least half of the food consumed by this group.

Feeding of Demersal Fish on Herring and Mackerel

One source of food for demersal fish is the feeding of the larger demersal species such as cod on herring (flow f in Fig. 1). Values of f (Table 3) are about 2 kcal·m^{-2}·yr^{-1} in the early 1960s and about one-third of this at the end of the 1960s.

Estimates of Transfer Efficiency through "Other Primary Carnivores" (ϵ_1)

The values obtained in Appendix Tables A1 and A2 can be used for estimating the transfer efficiencies ϵ_1 and ϵ_2 by taking account of the considerations depicted in Fig. 4. These efficiencies can be estimated in the following ways: for species such as sand eels, Norway pout, and sprats, $(P_2 + P_3)/(F_1 +$

TABLE 6. Estimates of "transfer efficiency" for application to "other primary carnivores."

Species	Stages	Option*					Reference diagram
		A	B	C	D	E	
Haddock	Larvae + pelagic juveniles	0.06	0.11	0.12	0.12	0.13	Fig. 4d
Herring (early 1960s)	Larvae + pelagic juveniles	0.01	0.10	0.12	0.06	0.12	Fig. 4c
(late 1960s)	Larvae + pelagic juveniles	−0.04	0.06	0.10	—	—	Fig. 4c
Sand eels	All stages	0.10	0.12	0.14	—	—	Fig. 4b

*Options A–C, assuming present-day levels of exploitation: A, assuming 90% initial mortality; B, assuming 50% initial mortality; C, assuming 0% initial mortality. Options D–E, assuming $Z = 0.2$; option D, assuming 90% initial mortality; option E, assuming 50% initial mortality.

$F_2 + F_1 - P_1$) (see Fig. 4b); for herring, mackerel, and haddock, $P_2/(F_1 + F_2 - P_1)$ (see Fig. 4c and 4d).

The values obtained by using these formulae are summarized in Table 6 for each of the five options A through E. Provided egg and first feeding mortality is no greater than 50%, the transfer efficiency through the fish component of "other primary carnivores" ranges from 6 to 14%. If all production were available for individuals in groups P and D, this would suggest an average transfer efficiency of about 10%, the same as the value proposed for food chain efficiency by Slobodkin (1961). However, some production will go to invertebrate secondary carnivores so that 10% may be an overestimate. Because the fish component of "other primary carnivores" may be as little as 50% or less (see above) it is possible that the transfer efficiency through "other primary carnivores" (in the sense of transfer from herbivore production to food for group P plus group D individuals) may be as low as 5%. The calculations shown in Table 3 and Fig. 2 have been done assuming values of ϵ_1 of 0.05 and 0.10. These lead to estimates of the percentage of herring and mackerel food coming from "other primary carnivores" ranging from 15–30% at the beginning of the 1960s to −12–35% at the end of the 1960s. An intermediate percentage would be reasonable and would be consistent with a value of transfer efficiency between 0.05 and 0.10.

Estimates of Transfer Efficiency from Group P to Group D (ϵ_2)

This transfer efficiency (ϵ_2) is equivalent to (flow from group P to group D)/(flow entering group P). Values for food and production for mature herring are shown in Appendix Table A1. From these it can be calculated that production/food = 15% at the beginning of the 1960s and 28% at the end. Natural mortality probably accounts for about 20–30% of total production at the beginning of the 1960s and 10–20% at the end. Estimates of ϵ_2 are therefore the following: early 1960, $\epsilon_2 = (0.15)(0.25) = 0.04$; late 1960, $\epsilon_2 = (0.28)(0.15) = 0.04$. A value of $\epsilon_2 = 0.04$ has therefore been used in the computations in Table 3 and Fig. 2.

Table 7 shows estimates of the ratios production/food calculated for each species and life history stage from the data in Appendix Tables A1 and A2. For larvae, the ratios are consistently high, ranging from 0.27 to 0.35. The actual values obtained in the simulations are largely dependent on the values assumed for the conversion efficiency of energy into growth. For example, Needham (1964), quoting Rubner, states that the gross efficiency of conversion of energy into growth in young, rapidly growing animals is about 35%. Slobodkin (1959), however, from a consideration of the chemical steps involved in food degradation, considered that an average growth efficiency of much more than 25% would be unlikely. The estimates obtained here may, therefore, be overestimated. For juveniles, the ratios are much more variable. Consideration of Fig. 3b shows that if the mortality of initial egg and first feeding larvae is extremely large, there may be little scope for further mortality if the biomass of the cohort is to attain a specified biomass at a given age. The small values of production/food for option A are therefore a direct consequence of the assumed high initial mortality rate of 90%. The negative value for sand eel juveniles effectively means that with 90% initial mortality, the biomass of a cohort would not be able to reach the specified amount by 2 yr of age even with zero juvenile mortality. Alternatively, if Fig. 3c represents the likely sequence of change in biomass with age, it would be possible for juvenile production to be relatively high irrespective of initial mortality. The ratio of production/food for juveniles can therefore range from very low to relatively quite high values. For mature animals the ratios of production/food range from 0.07 to 0.21. Small values apply to unexploited stocks when the total mortality rate is assumed to be relatively low ($Z = 0.02$). Higher values are possible for exploited stocks with higher values of Z. High values are possible because the process of recruitment adds to the biomass of the adult stock annually. The energy needed to make this possible is provided by food consumed during the larval and juvenile stages and does not have to be accounted for out of the food consumed by the adults.

The overall ratio of production/food for an entire life history depends on the relative importance of larvae, juveniles, and adults. Ratios higher than the value of 10% proposed by Slobodkin (1961) are theoretically possible, but only if there happens to be a large enough proportion of rapidly growing larvae and juveniles in the total population.

Relative Importance of Different Fish Groups

Table 5 shows the relative food requirements of different fish groups in the "other primary carnivores" group. The pelagic stages of demersal fish (including an allowance for "other species") require only 2–9 kcal·m^{-2}·yr^{-1} at the beginning of the 1960s and 3–16 kcal·m^{-2}·yr^{-1} at the end.

TABLE 7. Estimates of production/food for various life history stages.

	Stage	Option*				
		A	B	C	D	E
Haddock (early 1960s)	Larvae	0.33	0.34	0.34	0.35	0.35
	Pelagic juveniles	0.08	0.19	0.22	0.21	0.26
	Demersal juveniles	0.02	0.07	0.12	0.11	0.22
	Adults	0.21	0.21	0.21	0.08	0.08
Herring (early 1960s)	Larvae	0.30	0.31	0.32	0.31	0.32
	Juveniles	0.01	0.13	0.17	0.07	0.17
	Adults	0.15	0.15	0.15	0.07	0.07
Sand eels	Larvae	0.27	0.28	0.28	—	—
	Juveniles	−0.06	0.04	0.07	—	—
	Adults	0.21	0.21	0.21		

*See footnote to Table 6.

By comparison, the equivalent values for larval and juvenile herring and mackerel food are 22–71 and 12–33. For Norway pout, sand eels, and sprats (all life stages) the estimate for both periods is 25–32 kcal·m^{-2}·yr^{-1}. If biomass changes with age as indicated in Fig. 3c, somewhat larger values would be needed for demersal fish food. Even so, the indication is that, except perhaps seasonally and/or at certain places, the pelagic stages of demersal fish are likely to be relatively unimportant as food for potential predators. From a predator viewpoint, Norway pout, sand eels, sprats, and the young stages of herring and mackerel appear to make up a very much larger proportion of the available fish food.

Similar considerations apply to the relative importance of herring and demersal fish year-class strengths. From Appendix Table A2 it can be calculated that an average herring year-class in the early 1960s needed from 8 to 28 kcal·m^{-2}·yr^{-1} (net) during the "larval + juvenile" stages. An outstanding herring year-class such as that of 1956, which was about four times average, might therefore have required about 32–112 kcal·m^{-2}·yr^{-1}. This could represent up to more than half of the food consumption of the entire "primary carnivores" group under average conditons (Table 3). This suggests that there could have been a significant difference in the energy flow through this part of the system in that particular year.

By comparison, the strongest haddock year-class, that of 1967, was about 25 times average. If an average haddock year-class during the "pelagic stage" needs about 0.11–0.60 kcal·m^{-2}·yr^{-1} (net) determined from Appendix Table A1, then this year-class could have needed 3–15 kcal·m^{-2}·yr^{-1}. This is nearly as much as the amount required by an average herring year-class (Appendix Table A2). It seems likely therefore that relatively moderate fluctuations in herring (and mackerel) year-classes are more likely to be associated with significant variations in the ecosystem than the relatively much larger fluctuations that often occur in the year-class strengths of the demersal fish species.

Conclusions

Conclusions from this investigation are the following:

1) The food requirements of the commercially important fish species can be satisfied by the available food, without having to make any unreasonable assumptions.

2) This can be done for the two periods at the beginning and end of the 1960s, separately. At the end of the 1960s, when demersal stocks were larger, their increased food requirements could have been met theoretically via the pelagic part of the food chain.

3) To some extent, energy flows can be manipulated to allow unexploited stocks to be higher than present-day levels. It seems unlikely, however, that these could be as high as predicted by constant parameter "Beverton-and-Holt-type" calculations. In virgin stocks one may suppose that the value of M was higher than it is today and/or that recruitment levels were lower and/or that growth rates were lower.

4) Estimates of the food requirements of larval and juvenile fish depend critically on (a) the mortality of eggs and first feeding larvae and (b) the age at which a cohort attains its maximum biomass and how large this is compared with the biomass of the cohort at the age of first maturity. Estimates are given in the text.

5) Estimates of the fish component of the "other primary carnivores" group depend critically on considerations (4a) and (4b) above. If a cohort attains its maximum biomass at the age of first maturity, the fish component of the "other primary carnivores" group may be about 50%. If a cohort attains its maximum biomass before the age of first maturity, the fish component of the "other primary carnivores" group could be considerably higher. This would be a consequence of higher food requirements for the juvenile stages.

6) Transfer efficiencies (i.e. estimates of production/food) are different for different life stages). (a) For larvae, which are rapidly growing animals, transfer efficiencies could be theoretically similar to net growth conversion efficiencies (i.e. 25–35%). (b) For juveniles, theoretical values tend to be very variable. For example, if egg and larval mortality is very high, and maximum biomass is not reached until first maturity, there may be little scope for a high level of production if the cohort is to attain a specified biomass at first maturity. Alternatively, if maximum biomass is attained prior to first maturity, a relatively high production rate is theoretically possible between the age at which maximum biomass is attained and the age of first maturity. (c) For mature animals,

theoretical ratios of production/food ranged from 0.07 to 0.2. The smaller value is applicable to unexploited stocks with a low mortality rate ($Z = 0.02$). Higher values are possible for exploited stocks. This is because the mature stock is augmented annually by recruits, which have gained biomass at the expense of food consumed during the larval and juvenile stages. Thus, recruitment contributes to the production of adults. The higher the rate of exploitation, the higher is the theoretical value of production/food. (d) For an entire life cycle, the transfer efficiency depends on the relative proportions of rapidly growing juveniles and of slow growing adults. (e) For a particular species at a particular trophic level, the transfer efficiency also depends on the particular combination of life stages present at the particular trophic level. Estimates are given in the text.

7) Calculations suggest that because of the relatively large biomass of herring (as well as of mackerel), even relatively small fluctuations in year-class strength of these species are likely to be associated with bigger variations in the ecosystem than the relatively much larger fluctuations in demersal fish year-class strengths.

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Appendix 1

DETERMINATION OF THE ENERGY FLOWS IN FIG. 1

Let H and B be the energy provided annually by herbivores and benthic animals, respectively. Let P and D be the energy consumed annually by the adult pelagic and demersal groups, respectively. Then

(1) $a + b = H$
(2) $b + c = P$
(3) $d + e + f = D$
(4) $c + d = \epsilon_1 a$
(5) $e = B$
(6) $f = \epsilon_2 P$

where ϵ_1 is the proportion of the food consumed by "other primary carnivores" that is available for groups P and D, and ϵ_2 is the proportion of the food consumed by adult herring and mackerel that is available for group D.

The solutions to these equations are:

(7) $a = (H + B - P - D + \epsilon_2 P)(1 - \epsilon_1)$
(8) $b = H - a$
(9) $c = P - b$
(10) $d = D - B - \epsilon_2 P$

Appendix 2

Revised estimate of egg production per recruit

North Sea haddock

Age	F[1]	Z	e^{-Z}	Number[2]	Mean length	Weight[3] (g)	Fecundity[4]
2	0.38	0.58	0.560	10 000	28	108	80 000
3	0.57	0.77	0.463	5 600	33	323	140 000
4	0.68	0.84	0.432	2 593	37	456	210 000
5	0.79	0.99	0.372	1 120	40	576	270 000
6	1.0	1.2	0.301	417	44	767	380 000
7	1.0	1.2	0.301	125	48	995	510 000
8	1.0	1.2	0.301	38	50	1125	590 000
9	1.0	1.2	0.301	11			
10	1.0	1.2	0.301	3			

[1] Based on mean values of F from VPA during period 1959–68 ($M = 0.02$) (from Anon. 1976).
[2] Numbers in sea per 10 000 fish aged 2 yr.
[3] Mean lengths at spawning time (April 1).
[4] Weights = $0.009\ (\text{length})^{3}$.
[5] Fecundity = $196\ (\text{weight})^{0.9}$ (from Ratt 1932).

Number of eggs per 10 000 females aged 2 yr = 2.28×10^{7} (assuming only 50% spawn at age 2 yr) (i.e. $(5600 \times 0.8) \times (400 \times 1.4) \times (2593 \times 2.1) \times \ldots$).

Number of eggs per 2 yr-old fish of either sex = 1.14×10^{7} (assuming a 50:50 sex ratio).

The dry weight of a haddock egg is 0.076 mg (e.g. Hislop 1975).

The calorific value of a cod egg is 5.7 kcal·g^{-1}·yr^{-1} dry weight (Daan 1975).

The calorific value of the total egg production is therefore equivalent to 48 kcal per 2 yr-old fish (of either sex).

Mean number of 2 yr-olds = 2×10^{6} fish (from VPA for period 1959–70 and excluding the 1962 and 1967 year-classes).

Therefore total egg production of average year-class = 0.96×10^{10} kcal.

The area of the North Sea is taken as 0.57×10^{12} m^{2}.

Total egg production of an average year-class is equivalent to 0.017 kcal·m^{-2}.

Mean biomass of 2 yr-olds = $2 \times 200 \times 10^{6} = 4 \times 10^{10}$ g. The energy value (kcal) is also 4×10^{10} (assuming 1 g haddock = 1 kcal).

The biomass of 2 yr-olds is therefore equivalent to $4 \times 10^{10} / 0.57 \times 10^{12} = 0.070$ kcal·m^{-2}.

Total biomass of stock per 2 yr-old fish = 612 g = 612 kcal. Ratio of egg production/biomass = 48/612 = 0.08.

Appendix 3

Estimating Food Consumption

1) Young, Rapidly Growing Fish

Food required by a single individual — Let the rate of food consumption (F) of a fish of weight W be given by the expression

$$(1) \quad F\,dt = a_1 dw + a_2 W^{0.8}\,dt$$

The first term allows for the food required to take account of a growth increment. The second term takes account of the food required for maintenance.

For young, rapidly growing fish, individual growth is assumed to be exponential so that

$$(2) \quad W_t = W_0 \exp(Gt)$$

Then, from equation (2)

$$dw = GW_0 \exp(Gt)dt$$

Substituting for dw and W in equation (1) leads to

$$(3) \quad F\,dt = a_1 GW_0 \exp(Gt)\,dt + a_2 W_0^{0.8} \exp(0.8Gt)\,dt$$

This gives an expression for the consumption of food of an individual of age t during a time interval dt.

Food required by a total cohort — For simplicity, let the change in numbers at age be exponential also, so that

$$(4) \quad Nt = N_0 \exp(-Zt)$$

where Nt = number alive at age t. It follows that the biomass at age will also change exponentially, i.e. let

$$B_t = NW_t$$

where B_t = biomass at age t, then

$$(5) \quad B_t = N_0 W_0 \exp((G - Z)t)$$

The rate of food consumption of a cohort of N individuals is given by

$$(6) \quad NF\,dt = a_1 GB_0 \exp((G - Z)t)\,dt + a_2 N_0 W_0^{0.8} \exp((0.8G - Z)t)\,dt$$

The total food consumed (ψ) by the cohort while the individuals grow from age t_1 to age t_2 is given by

$$(7) \quad \psi = \int_{t_1}^{t_2} NF\,dt$$

Integration leads to

$$(8) \quad \psi = a_1 G(B_2 - B_1)/(G - Z) + a_2(B_2 W_2^{-0.2} - B_1 W_1^{-0.2})/(0.8G - Z)$$

where $B_1 = B_0 \exp((G - Z)t_1)$ = biomass at age t_1, $B_2 = B_0 \exp((G - Z)t_2)$ = biomass at age t_2, $W_1 = W_0 \exp(Gt_1)$ = weight at age t_1, and $W_2 = W_0 \exp(Gt_2)$ = weight at age t_2.

Production — Production (P) per cohort in time T is given by

$$P = Z \int_{t_1}^{t_2} B_t dt$$

$$(9) \quad = Z(B_2 - B_1)/(G - Z)$$

Computational notes — For computational purposes it is sufficient to know B_1, B_2, W_1, W_2, T, a_1, and a_2 to determine values for equations (8) and (9). Where

$$T = t_2 - t_1$$

$$(10) \quad G = (1/T) \ln(W_2/W_1)$$

and

$$(11) \quad Z = (1/T) \ln(W_2 B_1/W_1 B_2)$$

a_1 = 2.5 for larvae and 3.0 for older fish (equivalent to net growth conversion efficiencies of 40% and 33%, respectively), and a_2 = 5.9 per year (based on results obtained by Jones and Hislop 1958).

Computational results for successive juvenile stages are given in Appendix Tables A1 and A2.

2) Adults

Food for adults was calculated using equations (1) and (7), but with the differences that (1) the von Bertalanffy growth formula (von Bertalanffy 1938) was used for calculating dw and weight at age, and (2) the integration of equation (7) was performed by computer simulation, instead of algebraically.

To allow for food energy required by the developing gonad it is supposed that an individual with somatic weight W_t at time t grows and develops a gonad until, 1 yr later, its somatic weight is W_{t+1} whereas its total weight is W'_{t+1}. Immediately after spawning, total and somatic weight are both made equal to W_{t+1} (Fig. A1).

The drop in weight ($W'_{t+1} - W_{t+1}$) is due to the release of spawning products and is assumed to be equal to a certain proportion (p) of the somatic weight at spawning time

TABLE A1 Estimates of the food required by the young stages of haddock and sand eels

Haddock (early 1960s)

Stage[a]	Age (yr)	Avg weight (kcal)	Biomass[b] (kcal·m^{-2})					Food (kcal·m^{-2}·yr^{-1})					Production (kcal·m^{-2}·yr^{-1})				
			A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
1	0	0.0004	0.0017	0.008	0.017	0.014	0.07	0.048	0.20	0.41	0.34	1.58	0.016	0.068	0.14	0.12	0.55
2	0.22	1.0	0.0026	0.010	0.019	0.016	0.069	0.018	0.067	0.13	0.11	0.44	0.005	0.019	0.037	0.031	0.13
	0.33	7.0	0.0032	0.011	0.021	0.018	0.069	0.059	0.12	0.20	0.18	0.51	0.001	0.016	0.034	0.029	0.12
3	1.0	40	0.016	0.023	0.033	0.030	0.068	0.25	0.30	0.35	0.33	0.49	0.006	0.022	0.043	0.037	0.11
4	2.0	200	0.067	0.067	0.067	0.067	0.067	0.77	0.77	0.77	4.61	4.61	0.61	0.16	0.16	0.36	0.36

[a] Stages 1 through 4 corresponding to suffices for E and P in Fig. 4d

[b] A, biomass at 0 yr based on 98% egg mortality; B, biomass at 0 yr based on 50% egg mortality; C, biomass at 0 yr based on 0% egg mortality } $\ell = 0.8$ for fish > 2 yr

D, biomass at 0 yr based on 98% egg mortality; E, biomass at 0 yr based on 50% egg mortality } $\ell = 0.2$ for fish > 2 yr

$W = 1750$ g, $A = 0.24$

Sand eels

Stage[a]	Age (yr)	Avg weight (kcal)	Biomass			Food[b]			Production[b]		
			A	B	C	A	B	C	A	B	C
1	0	0.0001	0.38	0.90	1.8	9.18	37.5	68.9	1.49	10.5	19.54
	0.5	1.0	0.47	1.60	2.70						
2	2.0	9.0	9.0	9.0	9.0	37.90	57.5	70.3	2.2	2.01	5.20
3	>2.0					57.5	57.5	57.5	12.1	12.1	12.1

[a] Stages 1 through 3 corresponding to suffices for E and P in Fig. 4b

[b] Arbitrary units. A through C as for haddock. For fish > 2.0 yr, food and production calculated assuming $\ell = 1.0$, $W = 13$ g, $A = 0.86$

TABLE A2 Estimates of the food required by the young stages of herring (kcal·m^{-2})

Herring (early 1960s)

Stage[1]	Age (yr)	Avg weight (kcal)	Biomass A	Biomass B	Biomass C	Biomass D	Biomass E	Food[2] A	Food[2] B	Food[2] C	Food[2] D	Food[2] E	Production[2] A	Production[2] B	Production[2] C	Production[2] D	Production[2] E
1	0	0.001	0.058	0.29	0.58	0.12	0.59	1.60	7.03	13.99	3.07	13.41	0.48	2.19	4.22	0.95	4.24
2	0.33	1.0	0.095	0.37	0.67	0.17	0.66	1.89	5.60	9.22	2.96	9.07	0.32	1.19	2.10	0.57	2.07
2	1.0	20	0.25	0.59	0.89	0.35	0.87	0.78	1.72	2.47	1.12	2.44	0.058	0.21	0.39	0.057	0.37
2	1.33	34	0.35	0.73	1.00	0.52	1.00	4.77	6.48	7.49	5.60	7.49	0.30	0.39	0.85	0.018	0.85
2	2.33	104	1.56	1.56	1.56	1.56	1.56										
3	>2.33							18.4	18.4	18.4	38	38	2.8	2.8	2.8	2.6	2.6

[1]Stages 1 through 3 corresponding to suffices for I and P in Fig. 4c.
[2]For fish > 2.33 yr, food and production calculated assuming $Z = 0.5$ for options A, C and $Z = 0.2$ for options D and E. $W = 271$ g, $K = 0.38$

Herring (late 1960s)

Age (yr)	Avg weight (kcal)	Biomass A	Biomass B	Biomass C	Food[1] A	Food[1] B	Food[1] C	Production[1] A	Production[1] B	Production[1] C
0	0.001	0.026	0.13	0.26	0.75	3.28	6.29	0.22	1.01	1.96
0.33	1.0	0.047	0.18	0.33	0.96	3.03	4.86	0.16	0.60	1.06
1.0	20	0.13	0.35	0.50	0.48	1.10	1.52	0.023	0.073	0.14
1.33	34	0.25	0.50	0.67	3.93	5.17	5.87	0.40	0.077	0.38
2.33	104	1.4	1.4	1.4						
>2.33					8.1	8.1	8.1	2.25	2.25	2.25

[1]For fish 2.33 yr, food and production calculated assuming $Z = 1.0$, $W = 271$ g, $K = 0.38$

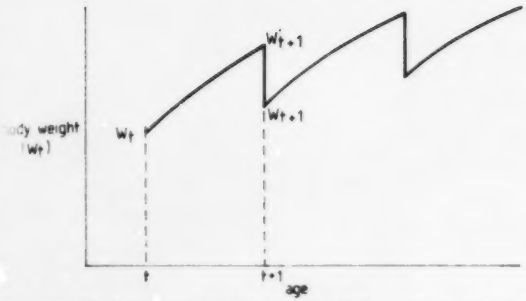

Fig. A1. Weight at age relationships for both somatic and total weights. W_{t+1} = somatic weight at age $t + 1$; W'_{t+1} = total weight at age $t + 1$.

(W'_{t+1}), i.e.

$$(W'_{t+1} - W_{t+1}) = pW_{t+1}$$

It is shown below that in this situation, segments of the curve for total weight at age (such as W_t to W'_{t+1}) can also be represented by a Bertalanffy curve, but with parameters K' and W'_∞. Expressions for calculating K' and W'_∞ are derived below.

Determination of growth parameters for total growth — Let the relationship between somatic weight and age be represented by a Bertalanffy growth curve, i.e.

$$W_t = W_\infty(1 - e^{-K(t - t_0)})^3$$

so that

$$W_t^{\frac{1}{3}} = W_\infty^{\frac{1}{3}}(1 - e^{-K(t - t_0)})$$

Elimination of t_0 leads to

$$(12)\quad (W_{t+1})^{\frac{1}{3}} = W_t^{\frac{1}{3}}e^{-K} + W_\infty^{\frac{1}{3}}(1 - e^{-K})$$

Now let

$$(13)\quad W'_{t+1} = W_{t+1}(1 + p)$$

where p is the energy content of the gonad expressed as a proportion of the somatic energy at the time of spawning.

Substitution of equation (13) into equation (12) gives

$$(14)\quad (W'_{t+1})^{\frac{1}{3}} = W_t^{\frac{1}{3}}Ae^{-K} + W_\infty^{\frac{1}{3}}A(1 - e^{-K})$$

where

$$A = (1 + p)^{\frac{1}{3}}$$

Manipulation of terms in equation (14) gives

$$(15)\quad (W'_{t+1})^{\frac{1}{3}} = W_t^{\frac{1}{3}}Ae^{-K} + \frac{W_\infty^{\frac{1}{3}}A(1 - e^{-K})}{(1 - Ae^{-K})}(1 - Ae^{-K})$$

This shows that total growth can also be represented by a Bertalanffy curve, but with parameters K' and W'_∞ where K' satisfies the relationship

$$e^{-K'} = Ae^{-K}$$

so that

$$(16)\quad K' = K - \ln A = K - \tfrac{1}{3}\ln(1 + p)$$

and

$$(17)\quad (W'_\infty)^{\frac{1}{3}} = W_\infty^{\frac{1}{3}}A(1 - e^{-K})(1 - Ae^{-K})$$

$$= W_\infty^{\frac{1}{3}}(1 + p)^{\frac{1}{3}}(1 - e^{-K'})(1 - e^{-K})$$

so that from equation (15)

$$(W'_{t+1})^{\frac{1}{3}} = W_t^{\frac{1}{3}}e^{-K} + W'^{\frac{1}{3}}_\infty(1 - e^{-K})$$

This equation is of the same form as equation (12), but with K and W_∞ replaced by K' and W'_∞.

Computational notes — For the adults, computations were done using the following parameter values: $a_1 = 3.0$ and $a_2 = 5.9$ per year (see equation (1)) (based on results in Jones and Hislop 1978); $p = 0.16$ for haddock (based on results in Appendix 1 and assuming that the energy requirements of males are equivalent to those of females); for herring and sand eels, a value of $p = 0.25$ was adopted (based on data in Jones and Johnston 1977).

Computational results for adults are given in Appendix Tables A1 and A2.

Simple Models of Predation in Multi-age Multispecies Fisheries for Considering the Estimation of Fishing Mortality and its Effects

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POPE, J. G., AND B. J. KNIGHTS. 1982. Simple models of predation in multi-age multispecies fisheries for considering the estimation of fishing mortality and its effects, p. 64–69. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

A simplistic model of predation is proposed; this is used to develop a tractable multispecies cohort analysis for estimating fishing mortality, predation mortality, and population numbers from multispecies catch at age data. An application to some North Sea species data illustrates the method. The problems of developing a suitable model of yield in multispecies fisheries are discussed and several simple models suggested.

Key words: multispecies fisheries, cohort analysis, predation, food preference, mortality, steady-state yield

POPE, J. G., AND B. J. KNIGHTS. 1982. Simple models of predation in multi-age multispecies fisheries for considering the estimation of fishing mortality and its effects, p. 64–69. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

Nous proposons un modèle simple de prédation : on s'en sert pour mettre au point une analyse des cohortes d'espèces multiples traitable, permettant d'estimer la mortalité par pêche et par predation ainsi que l'importance des populations à partir de données sur les prises par âge d'espèces multiples. A titre d'exemple, nous appliquons la méthode a des données sur certaines espèces de la mer du Nord. Nous examinons les problèmes que pose l'élaboration d'un modèle adéquat de rendement de pêche d'espèces multiples et suggerons plusieurs modèles simples.

Introduction

Models of multispecies fisheries systems tend to be of two types. The simpler type (Larkin 1963; Pope 1979) is based on extensions of the Schaefer (1954) model of fisheries. The more elaborate type, for example, that of Andersen and Ursin (1977), is the multispecies extension of the Beverton and Holt (1957) model that takes into account the age cohort structure of fisheries. Both approaches have their advantages. The quadratic structure of the Schaefer models makes it comparatively simple to gain insights into the behavior of the model, even where many species are involved. Moreover, optimization can be performed using quadratic programing methods. The problem, however, with extended Schaefer methods is that parameter fitting is achieved through regression techniques and the number of parameters is a function of the square of the number of stocks. Clearly the difficulties of parameter estimation become quite serious with a model of only a few species.

A secondary problem with these models is that, although they might describe the steady-state situation quite well, they fail to account for year-class size effects and it is doubtful whether they describe transitional states with any accuracy. Consequently stability analyses based on them are dubious. A further effect of the failure to take account of individual year-class effects is the impossibility of predicting the effect of mesh changes. Because this might be a prime method of management for some mixed fisheries, this is a very real disadvantage.

Conversely, cohort models do not suffer from these disadvantages to quite the same degree because such interactions might be inferred from the biological behavior of the animals. Having said this, the actual process of charting all interactions between all ages of all species considered might well prove a daunting task, because the number of interaction terms would increase with the number of cohorts. Moreover, some small but potentially important interactions might be masked by noise, whereas others would be hidden by other correlated processes. A further problem with such reductionist techniques is that uninvestigated correlations may exist between estimates of various parameters and these may lead to wrong conclusions when the model is used to extrapolate. The major disadvantage of these models, however, is that realism has been bought at the expense of mathematical tractability. This results in models from which it is difficult to explore more than one set of options at a time using computer simulation techniques. As a result such models tend to be opaque.

Clearly, models that maintain some of the mathematical tractability of the multispecies Schaefer (1954) models but are able to consider the cohort structure of the Beverton and Holt (1957) models could be most valuable. In practice, such tractability is only likely to be bought at the price of drastic simplifications. Thus this report suggests assessment methods based on a simple predation model with the intention of easing the problems of both estimating mortality rates and considering their effects in multi-age multispecies fisheries.

A Simple Model of Predation

It is natural to consider predator ration as increasing with

prey abundance to some asymptotic level. At this asymptote, predation can be thought of as a removal of a block of prey biomass equal to some proportion of predator biomass. If weight at age is taken as a constant for prey and predator then this simplifies to the removal of a certain number of prey by each predator.

Thus, if $P(i)$ is the number of prey at age i and $Q(j)$ is the number of predators, then considering only predation by one age of predator on one age of prey,

$$(1) \quad P(i+1,t+1) = P(i,t) - \alpha(i,j)Q(j,t)$$

where $\alpha(i,j)$ is the number of prey eaten by a single predator.

Equation (1) can be extended in an obvious fashion for other ages or species of predator and the effect of multiple prey species can be modeled by assuming the predators' ration to be divided between the prey in proportion to their biomass and possibly a prey preference factor. This model of predation will of course break down at low prey numbers but its simplicity enables various problems to be modeled in a succinct manner.

A Modified Cohort Analysis in which Constant Natural Mortality is Replaced by Estimates of Predation Levels

The feeding (predation) model outlined above leads to a simple method of calculating fishing mortality, natural mortality, and population numbers from the available catch at age data of a range of species. Estimates of feeding rate of predators and of the preferences that various ages of predators have for various ages of prey are used in the method to calculate how many of each age of each species are devoured by older ages of the same species or by other species included in the analysis.

Consumption figures for each age of each species are calculated for each year in turn, starting from the most recent, using population levels of predator and prey calculated by a method analogous to cohort analysis. The underlying assumptions are that the fish in the analysis get a ration from the other fish in the analysis. This is constant from year to year and it is taken from all prey cohorts in proportion to the relative biomass that each prey cohort forms of the suitable prey array.

A suitable prey array is defined by a preference matrix which with present knowledge can do little more than ensure that big fish are not eaten by small fish. As with the predation model, the model chosen does not consider the possibility of variations in total ration size with variations in prey abundance or the possibility that differing proportions of the diet might be taken from food sources other than those quantified in the analysis. For example, a run based on cod, haddock, whiting, saithe, herring, and plaice in the North Sea would consider that an 8-yr-old cod had a need for X kg of food per year, of which $Y\%$ would always be met from younger ages of cod and from suitable ages of haddock and whiting, saithe, herring, and plaice. With such a model it is clear that the natural mortalities estimated will be tentative. The method should, however, be useful for estimating maximum and minimum levels of mortality.

As with single species cohort analysis, fishing mortalities (F) for the oldest age of each cohort of fish have to be specified. These are used to estimate average populations in the final year as

$$(2) \quad \bar{P}(i,y) = C(i,y)/F(i,y)$$

where y is the terminal year, C is catch numbers, and $\bar{P}$ the average population. The total ration of the jth cohort is taken as

$$(3) \quad \bar{P}(j,y)X(j)Y(j)/100$$

where X and Y are as defined for 8-yr-old cod above. This ration is taken to be composed of the various other cohorts of fish in the analysis such that the amount taken from the ith species/age is proportional to

$$(4) \quad \bar{P}(i,y)A(i,j)W(i)$$

where $A(i,j)$ is the preference that predator cohort j has for prey cohort i and $W(i)$ is the average weight of the prey cohort i. Using equations (2)–(4), the numbers of each cohort eaten by each other cohort are calculated. These are then used to estimate P, the population at the beginning of the year, and hence the total mortality. For nonterminal years (t) the analysis proceeds using a simple cohort analysis type formula

$$(5) \quad P(i,t) = \{C(i,t) + D(i,t)\}\exp(M/2) + P(i+1,t+1)\exp(M)$$

where C and D are the numbers of fish caught and devoured, respectively, in year t and M is a constant level of natural mortality from other sources; $D(i,t)$ is the sum of the numbers of prey age i eaten by all predators in year t. The values of $P(i,t)$ used in these equations are initially estimated as

$$(6) \quad \bar{P}(i,t) = \{P(i+1,t+1) + 0.5C(i,t)\}\exp(M/2)$$

Estimates of $D(i,t)$ are then calculated and the $P(i,t)$ is calculated using equation (5). A new estimate of $\bar{P}(i,t)$ is then obtained and a fresh estimate of $D(i,t)$ is made. This iterative process is continued until the iteration where

$$\sum_{\text{all } i} \{\dot{Z}_t(i) - Z_t(i)\}^2 \leq 0.1 \times 10^{-n}$$

and where $\dot{Z}_t(i)$ and $Z_t(i)$ are the total mortality in ith cohort in the tth year estimated in the current and the previous iteration. The convergence of this process is very rapid.

For illustration purposes an analysis was made with the catch at age data for cod (ages 0–8), haddock (0–8), whiting (0–7), saithe (0–11), herring (0–8), and plaice, female (0–14) and male (0–9), for the years 1963–77 as given in various ICES Working Group reports. The average weights of the fish were those given by the Working Groups. For maximum simplicity in the test run it was assumed that the preference $A(i,j)$ of the various ages (j) of cod, whiting, and saithe for the prey species ages (i) was (with the exception of haddock) given by

$$(7a) \quad A(i,j) = 0.5 \text{ if } 0 = i \leq k(j)$$

TABLE 1. Maximum age (years) of each prey species for each age of predator (cod, whiting, and saithe).

Predator age	Maximum age of prey						
	Cod	Haddock	Whiting	Saithe	Herring	Plaice ♀♀	Plaice ♂♂
Cod							
1	0	0	0	—	0	0	0
2	0	1	1	—	0	0	0
3	0	2	2	—	2	1	1
4	0	3	5	—	8	2	2
5	1	4	6	—	8	2	3
6	1	5	7	—	8	3	4
7	2	6	7	3	8	3	4
8	2	7	7	4	8	4	5
Whiting							
1	0	0	0	—	0	—	—
2	0	0	0	—	0	—	—
3	0	0	0	—	1	—	—
4	0	0	0	—	2	—	—
5	0	0	0	—	3	—	—
6	0	0	0	—	3	—	—
7	0	0	1	—	3	—	—
Saithe							
1	—	—	—	—	0	—	—
2	0	0	0	—	8	—	—
3	0	1	1	—	8	—	—
4	1	1	1	—	8	—	—
5	1	2	1	—	8	—	—
6	1	2	1	—	8	—	—
7	1	2	1	—	8	—	—
8	1	2	1	—	8	—	—
9	1	2	1	—	8	—	—
10	1	2	1	—	8	—	—
11	1	2	1	—	8	—	—

(7b) $A(i,j) = 1.0$ if $0 < i \leq k(j)$

(7c) $A(i,j) = 0.0$ if $i > k(j)$

where $k(j)$ is the integer in the jth column position in the row of Table 1 appropriate to the prey and predator. For example, $k(5)$ for cod-eating cod is 1; thus 5-yr-old cod are given a preference of 0.5 for 0-group cod, 1.0 for 1-group cod, and 0.0 for all other ages of cod. The $k(j)$ thus specify the maximum age of prey which can be eaten by the jth age of predator. The preferences of cod and whiting for haddock were modified to half that given by equation (7) to take account of area distribution effects. 0-group plaice and 0- and 1-group saithe, which are seldom found in the open sea, were exempted from predation. It must be stressed that these preferences are only illustrative. True preferences would take into account area distribution and feeding preferences.

Predators' rations were assumed to be related to body weight. Thus all ages of cod of 1 or more were taken to have an annual diet in which 40% of their average weight was taken from the fish in the analysis. Similarly, predation by whiting and saithe was considered to be 20% and 4% of body weight, respectively. The low figure for saithe resulted from English groundfish survey observations which suggest that saithe mostly prey on Norway pout. In addition to predation mortality, a fixed natural mortality (M) of 0.1 was used on all ages of all species.

Table 2 shows the average (1963–77) natural mortality at age for each species in the analysis. For all ages over 1 this is not substantially different from the conventional levels and consequently the estimates of fishing mortality and population sizes for these ages are substantially the same as given by the responsible ICES Working Groups. Consequently they are not shown here. It would seem that estimates of population sizes and fishing mortality generated by standard virtual population analysis (VPA) techniques for these species are unlikely to be seriously in error. This might not be the case, however, for stocks such as Norway pout where the F/M ratios are lower.

The natural mortalities calculated in this analysis are of course sensitive to the ration levels and preferences adopted. The preferences affect the results directly and a suitable way of estimating these will have to be found. Ideally a complete enumeration of predation deaths each year would solve this problem but this would hardly seem to be a realistic approach. One possibility would be that quantitative stomach analyses be made for cod, whiting, and saithe in a similar fashion to the results given by Daan (1975) for cod. This work would need to estimate the numbers of each age of prey species eaten by each age of predator during one particular year on a stock-wide basis. Preferences could then be adjusted to reproduce these consumption levels in the multispecies cohort analysis.

This could be done when a sufficiently long series of catch at age data for future years has accumulated, perhaps after 5 yr.

Consideration of the recruitment figures generated by this method does not reveal any clear relationship between these and the spawning stock biomasses for cod, haddock, or whiting. The range of cod spawning biomasses in the years in question may not have been sufficient to make this obvious. It is possible that higher levels of cannibalism by cod resulting from higher stock sizes might obscure a stock–recruitment relationship; that is to say, apparent constant recruitment at age 1 might result from a large stock producing more recruits and eating more of them. The annual results for natural mortalities on 0-group cod (age 0.5–1) vary from 0.59 in 1967 to 1.46 in 1975. Thus differences in predation levels of 0.87 would lead to survivals which vary by a factor of more than 2 between some years. Thus a working group estimating population size using standard VPA with a constant natural mortality would see the effects of predation in reduced recruitment estimates. One possible way to tackle the problem would therefore be to consider predation as a part of the stock and recruitment problem and to continue to work as though natural mortality was constant. Changes in natural mortality on young fish might be monitored using groundfish survey results and it would be interesting to compare these figures with the estimates obtained by the cohort analysis presented here and with the results of the more detailed model suggested by Helgason and Gislason (1979).

Investigating the Behavior of Multi-age Multispecies Predation Models

Complex multispecies fisheries systems have generally been investigated in the past using computer simulations. Andersen and Ursin (1977) present such a model for the North Sea. A similar but simpler model can be developed by reversing our cohort analysis model. Such models allow projections to be made forward in time and to discover the steady states that correspond to various fisheries inputs. Simulations are, however, time-consuming and can only provide answers for one set of inputs at a time. To investigate the effect of independent changes in the various inputs, therefore, requires a factorial experiment where each simulation run provides the results for just one cell. Thus, by their nature, simulations tend to be a painstaking way of investigating the behavior of complex systems. It is, therefore, interesting to consider if there are any more direct paths to enlightenment about the behavior of such systems.

The simple constant predation model of the preceding section leads to equations of state similar to those of the extended Leslie matrices investigated by Pope (1976). The basic structure of Leslie's matrix (Leslie 1948) accounts for mortality and fecundity effects in an age-structured population but contains no negative feedback features. In general, therefore, it does not lead to steady-state solutions although stable age structures do emerge with time.

Pope (1976) showed various extensions of this approach to make it more "fishy." The most fundamental of these changes was to extend the matrix by a row and a column. This enabled a constant term to be added to the recruitment equation, thus ensuring that unity is an eigenvalue of the matrix.

TABLE 2. Average natural mortalities* generated by the multispecies cohort analysis.

Species	Run	Ages (yr) 0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Cod	1	0.975	0.206	0.104	0.1	0.1	0.1	0.1	0.1	0.1						
Haddock	1	0.847	0.403	0.242	0.115	0.108	0.104	0.102	0.1	0.1						
Whiting	1	1.114	0.405	0.149	0.131	0.131	0.131	0.118	0.109							
Saithe	1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1			
Herring	1	0.407	0.271	0.260	0.220	0.218	0.219	0.193	0.143	0.143						
Plaice ♀♀	1	0.1	0.117	0.109	0.103	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Plaice ♂♂	1	0.1	0.117	0.109	0.106	0.103	0.1	0.1	0.1	0.1	0.1					

*These mortalities include a component of nonpredation mortality set at 0.1 for all ages of all species.

Consequently the extended matrix has a steady-state solution. Additionally, whether or not this steady state is a stable equilibrium can be shown to be dependent on whether the eigenvalue of the embedded Leslie matrix is greater or less than unity. A further extension is to allow for predation using negative entries in the matrix, and this gives equations similar to equation (5). For example, the equation for the population of a prey species of age i, $P(i,t)$, in year t would become

$$(8)\quad P(i,t) = P(i-1,t-1)S - \alpha(i,j)Q(j,t-1)$$

where S is the survival rate for nonpredatory mortality, $\alpha(i,j)$ is the number of prey eaten in the period by one predator, and $Q(j,t-1)$ is the population of a predator of age j in year $t-1$.

The problem with this extension is that in a simulation $P(i)$ may become negative as a result of predation. If negative values are replaced by zero then simulations can of course be continued. More interestingly, the existence of negative values in the steady-state solution (the first eigenvector) would seem to indicate that no steady state exists, although the stocks might continue to oscillate about with various ages of prey species becoming zero at various times. When steady-state conditions are considered these problems can be better dealt with by dropping the Leslie matrix approach and by using linear programing (LP).

For example, the simple extended Leslie matrix

$$(9)\quad P(1,t) = g + P(2,t-1)f$$

$$(10)\quad P(2,t) = P(1,t-1)s$$

where g, f, and s are constant recruitment, fecundity, and survival terms, respectively, can be recast as the LP problem maximize $P(1) + P(2)$ subject to the two equality constraints

$$(11)\quad P(1) - P(2)f = g$$

and

$$(12)\quad P(2) - P(1)s = 0$$

Clearly this approach has some benefits. LP usually implies the additional constraints $P(1) \geq 0$, $P(2) \geq 0$. The system could moreover be extended by replacing $P(1)s$ by $P(1) - C(1)$, where $C(1)$ is the catch number. The LP could then be used to maximize catch subject to the modified constraints. Where a steady state exists its stability could be considered by an LP with small perturbations in $P(1)$, $P(2)$ of $\Delta P(1)$, $\Delta P(2)$ as the variables. This would be framed as a problem to maximize $\Delta P(1)$ and $\Delta P(2)$ subject to the constraints

$$(13)\quad \Delta P(1) \leq f\Delta P(2)$$

and

$$(14)\quad \Delta P(2) \leq -s\Delta P(1)$$

The solution of this LP problem would show if $\Delta P(1)$ and $\Delta P(2)$ are constrained at all. If they are not, then clearly the steady state is not stable. Equations (13) and (14) are of course equivalent to the condition that the principal eigenvalue of the embedded Leslie matrix be less than 1. It would seem, therefore, that LP might be quite a useful way of handling simple predation-linked cohort models.

The great limitation of this approach would be the restriction that a particular age of predator could only have one prey. With more than one prey the steady-state equations cease to be linear and LP could not be used to solve the full problem. Where a predator Q eats two prey species P and R with equal preference the steady-state equations become

$$(15)\quad P(2) = P(1)s - \frac{P(1)}{P(1) + R(1)} \times Q(j)$$

and

$$(16)\quad R(2) = R(1)s - \frac{R(1)}{P(1) + R(1)} \times Q(j)$$

These, of course, can be combined to give one linear equation so that LP might still play a useful part in solving subproblems, with other forms of programing being used to solve the nonlinear constraints such as those of equations (15) and (16). For more complex problems a nonlinear programing approach might have to be used. In either case the use of a mathematical programing approach would seem to offer an attractive approach for considering the optimal configurations of multi-age multispecies systems.

Discussion

Considering forms of predation based on constant diet enables various simple approaches to be used to study multispecies fisheries. Certainly it facilitates the construction of multispecies cohort analysis. This enables coarse estimates to be made of predation-induced natural mortality. Estimates made for some North Sea species indicate that these are low on older ages. Therefore the estimates of fishing mortality made by standard VPA are not likely to be seriously in error for these species. The method moreover indicates new ways in which stomach content data might be collected and analyzed.

Constant predation models also allow simple multispecies systems to be modeled using Leslie matrices and/or linear programing. These would enable steady states, optimum states, and stability to be considered more simply than can be achieved by simulation. Moreover, the simple structure and general availability of linear programing packages should make the transfer of models and data sets straightforward. These linear approaches are limited to comparatively simple predation situations and would have to be replaced by a nonlinear programing approach to deal with a system like the North Sea. Such models should be developed and their behavior contrasted with the more realistic but less tractable simulation models.

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Resource Assessment and Evaluation of the Dynamics of the Fisheries Resources in the Northeastern Pacific with Numerical Ecosystem Models

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The development of offshore fisheries in the vast northeastern Pacific is relatively recent. Exploratory surveys in the late 1950s demonstrated the abundance of groundfish in this region. The resource surveys in the large area are expensive and without an inordinately large field effort the accuracy of the results is low. Due both to the lack of conventional fisheries and biological data and the inherent shortcomings of single species models, those models are of questionable value for managing the multination, multispecies fisheries of the northeastern Pacific Ocean. Two biomass-based, holistic, ecosystem models, PROBUB and DYNUMES, are being developed and are used at Northwest and Alaska Fisheries Center (NWAFC) in Seattle for the evaluation of the abundance and dynamics of the fishery resources and for the study of the response of these resources to exploitation and to environmental changes (anomalies). We describe the general background of these models. We include equilibrium biomasses, as computed with the PROBUB model for the eastern Bering Sea and the western Gulf of Alaska. These are compared with conventional trawling surveys results, which have been converted with catchability and availability factors. The nature of the dynamics of the biomasses in space and time is briefly described and the effects on the resource assessment are demonstrated with some results from the DYNUMES model.

Key words: fish ecosystem, ecosystem dynamics, ecosystem modeling, northeastern Pacific fisheries resources.

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La pêche hauturière dans le vaste Pacifique nord-est est un développement récent. Des relevés d'exploration à la fin des années 1950 avaient démontré qu'il y avait dans cette région abondance de poissons de fond. Les relevés des ressources de régions aussi étendues sont dispendieux et, à moins qu'on y consacre un effort démesuré sur le terrain, la précision des résultats laisse à desirer. Les modèles sur lesquels fonder les pêches d'espèces multiples, pratiquées par plusieurs nations dans le Pacifique nord-est, ont une valeur douteuse, tant à cause du manque de pêcheries traditionnelles et de données biologiques que des défauts inhérents aux modèles d'espèces uniques. On est à mettre au point deux modèles holistiques d'écosystèmes, fondés sur la biomasse, PROBUB et DYNUMES. On les utilise au Northwest and Alaska Fisheries Center (NWAFC), à Seattle, pour évaluer l'abondance et la dynamique des ressources halieutiques et pour étudier les effets de l'exploitation et des changements environnementaux (anomalies) sur ces ressources. Nous décrivons les éléments de base de ces modèles, y compris les biomasses d'équilibre de la mer de Béring et de l'ouest du golfe d'Alaska, telles que calculées à l'aide du modèle BROBUB. Nous comparons ces données avec celles de relevés par chalutage, ces dernières étant ajustées à l'aide d'un facteur de potentiel de capture et de disponibilité. Nous décrivons brièvement la nature de la dynamique de la biomasse dans l'espace et dans le temps et démontrons les effets de l'évaluation de la ressource, avec quelques résultats obtenus à l'aide du modèle DYNUMES.

Characteristics of the Northeastern Pacific Fishery Resources and their Exploitation

The northeastern Pacific fishery area consists of three different regions — the eastern Bering Sea, the Gulf of Alaska, and the North American coast from Vancouver Island, British Columbia, southward to Point Conception, California. The Bering Sea is considerably different from the other two regions; it has a large continental shelf (twice the size of the North Sea) and has pronounced seasonal changes, including partial ice cover during winter. The northeastern Pacific is, in general, a biologically rich area and contains great herds of marine mammals. The most abundant fish species undertake migration in the northeastern Pacific.

Although limited coastal fisheries developed in the 19th century along the coasts of the northeastern Pacific, development of the modern large-scale offshore fishery started only in the 1960s by Japanese and Soviet fishing fleets. The maximum catch from the eastern Bering Sea was 2.2 million t in 1975, consisting mainly of walleye pollock (*Theragra chalcogramma*) and flatfish. The highest catch from the Gulf of Alaska was 380 000 t in the late 1960s consisting primarily

of Pacific ocean perch (*Sebastes alutus*). About 200 000 t of Pacific hake (whiting) (*Merluccius productus*) and rockfish were caught annually off the Washington and Oregon coasts by foreign fleets in the late 1960s.

Intensive investigations have been carried out on Pacific halibut (*Hippoglossus stenolepis*), and its fishery has been regulated from the early 1930s. The five species of Pacific salmon have also been well investigated in the last half century, and their fishery is also regulated. The exploratory surveys of demersal fishery resources were carried out in the 1950s (Alverson et al. 1964), wherewith the general abundance and distribution of these resources was ascertained but, with the exception of salmon and Pacific herring of the Canadian coast, the pelagic resources are as yet unexplored.

The most pressing present-day fisheries research problem in the northeastern Pacific is the assessment of the state (magnitude) of the fish stocks and their fluctuations, and such information is required for fisheries management of the "200-mile fisheries conservation zone," including resource allocation to foreign countries. In addition, much additional basic information is needed for all species, such as spawning areas and time, growth rates, food composition and its variation, year-class strengths, etc. The knowledge on the distribution and migrations of juveniles is also missing. In respect to specific knowledge on species-specific data and to knowledge on abundance and distribution of species, exploration and assessment in the northeastern Pacific is several decades behind that in the North Atlantic. Excluding the Canadian coast and some limited coastal areas in Alaska, the fisheries resource research is at present largely carried out by one laboratory with limited personnel and ship availability.

Conventional Means of Resource Assessment in the Northeastern Pacific, Results and Limitations

In recent years regular trawling surveys have been carried out in the eastern Bering Sea during the summer months and more occasionally in the Gulf of Alaska and along the west coast of North America. These expensive surveys provide only a general picture of the abundance and distribution of species vulnerable to capture with a bottom trawl. In general, the accuracy of trawling survey results is at best ±50% (Grosslein 1976). For example, the 1975 trawling survey estimated the walleye pollock biomass (exploitable) in the eastern Bering Sea to be 2426 000 t. The corresponding mean value for the 1976 survey was only 679 000 t (Bakkala and Smith 1978). Corresponding values for yellowfin sole (*Limanda aspera*) were 1039 000 and 2095 000 t, and for Pacific cod 64 000 and 102 000 t, whereas the all nation commercial catch of cod from the same area was 57 000 t. The reasons for the discrepancies are several; among the main causes are migrations in and out of the area and the existence of considerable biomasses of semidemersal fish over deep water, where they live a pelagic life and feed heavily on euphausids.

Although various single species stock assessment models have been applied to evaluate the resources of various northeastern Pacific commercial species, the results of such applications are less reliable in the northeastern Pacific than in some other well explored and exploited areas, such as the North Atlantic. The reasons for this are several: for example, the virtual population analysis (VPA) is not fully applicable, because (a) the catch statistics and length–age frequency distribution data are haphazardly and incompletely collected, (b) most species undertake pronounced seasonal and "life cycle" migrations, (c) the "natural" mortality rate estimates are very unreliable, (d) most species are underexploited, and (e) there is heavy consumption of fish by mammals (the mammals consume twice as much fish in the eastern Bering Sea as the total commercial catch).

Similarly, any other available single species model is not fully applicable to the stocks in the northeastern Pacific, because either initial stock size is not known, data for year-class strength determination is deficient, natural mortality is variable and not known, and fisheries statistics are deficient. Furthermore, the main general shortcoming of single species approach is that each species is treated as an independent entity. However, there is an intensive interspecies interaction, mainly via predation (i.e. fish eat fish). The analysis of shortcomings of past resource assessment models (including a recent analysis of these problems by Dickie (1979)) and the review of types, availability, and reliability of basic data of northeastern Pacific fish and fisheries suggested that a synthetic and holistic approach for resource evaluation must be taken in which use is made of all available data and knowledge.

Objectives and Principles of Ecosystem and Multispecies Simulation Models

It might be useful to differentiate between various types of models and simulations (models). Conventionally, a model has been considered to be an abstraction and simplification of a given condition and/or process, whereas a simulation is a numerical reproduction of a system of conditions and processes, based on available empirical data and knowledge and may contain many tested models.

The objectives of our numerical ecosystem simulations can be grouped into two main categories: (1) investigative and digestive (analytical) objectives, including basic ecological research, that permits quantitative determination of the state of the ecosystem, determination of the effects of environmental changes and interspecies interactions in space and time, and the establishment of research priorities; (2) general management guidance, the assessment of fisheries resources, and the determination of the effects of the exploitation on these resources.

The following basic principles have been followed in our ecosystem simulation. (1) The ecosystem simulation must include all of the essential biological and environmental interactive components of the system. (2) The ecosystem simulation should have proper space and time resolution (i.e. be three- to four-dimensional (two to three space and one time dimension)) and must have a diagnostic as well as a prognostic phase. (3) Theoretical conceptualizations should be avoided, unless they have been tested with empirical data and proven to be valid. (4) Explicit approaches, free from mathematical artifacts, should be preferred (i.e. the mathematical formulas used in the model must reproduce known processes rather than assuming that a mathematical formula represents

the behavior of a system). (5) Biomass balance and trophodynamic computations should start with apex predators (including man); these can be treated as "forcing functions" of the system.

It has been amply demonstrated in the past that the start of trophodynamic computations from the lower end (i.e. basic organic production) does not lead to reliable quantitative results because the pathways of basic organic production to secondary and tertiary production are very variable in space and time and not fully known quantitatively. Many separate plankton production models exist, which try to alleviate these shortcomings.

In addition, the following requirements apply to ecosystem simulations which emphasize the "fisheries ecosystems": (1) The simulation must be capable of solving the major part of the age-variable mortalities (especially predation, spawning stress, and fishing mortalities). (2) There must be a unique solution to the system of basic equations in defined conditions (for determination of the "equilibrium biomasses"). (3) The system of equations should not be conditionally stable (except for unique solution in defined conditions).

Biomass-based Ecosystem Simulation Models in NWAFC (PROBUB and DYNUMES)

Most available population dynamics models are number based. This usually requires that each species must be divided into age-groups to which initial numerical strength must be assigned and separate continuous bookkeeping for each age-group must be carried out in the model. The distribution of numbers in juvenile stages is, however, usually unknown. Furthermore, there must be frequent conversion between numbers and weight (biomass), as growth rate is highly age dependent. In addition, predation is a highly predator–prey size (viz. age) dependent process.

Considering the practical (computational) complexities of number- and biomass-based models, it was decided to use a biomass-based simulation model for marine ecosystem simulation. The Anderson–Ursin (1977) multispecies model is essentially a number-based model and is applicable to areas where basic input data on species are readily available (e.g. the North Sea). It is not possible to describe the complex models here in detail, but to present only the essentials of the models with a "skeleton model" (see Appendix). The full models have been documented by Laevastu and Favorite (1978a, b).

A schematic flow diagram of the computations in the skeleton model is given in Fig. 1. This model and the equations used in it are briefly described in the Appendix. Some of the dynamic aspects of a marine ecosystem, which must be included in any dynamic simulation model, are shown in Fig. 2.

The dynamical–numerical marine ecosystem model (DYNUMES) is a gridded model (for grid see Fig. 3A), which allows detailed computation of dynamics. All computations are carried out at each grid intersection (grid point) at each time step (week or month). The prognostic bulk biomass model (PROBUB) is a simplified version of DYNUMES, where computations are carried out in each defined area ("box") (see Fig. 3B).

Initial first guess biomass is used as the computation base in the first time step (Fig. 1). Before computing biomass

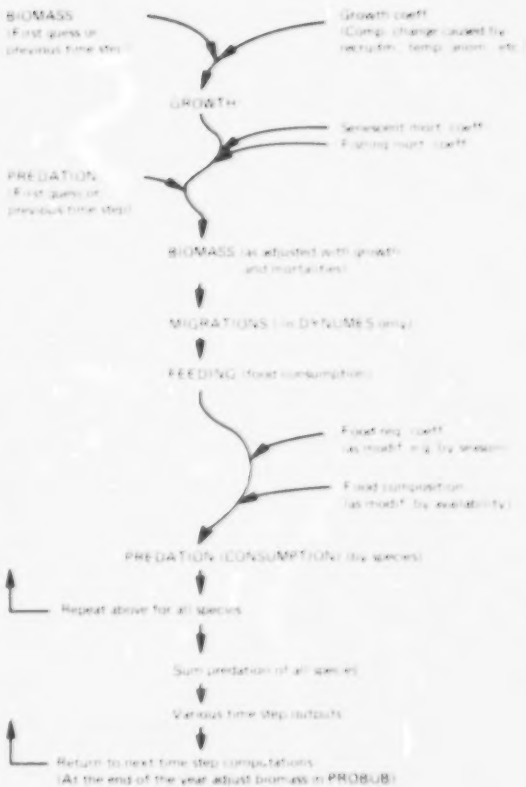
BIOMASS
(First guess or previous time step)
Growth coeff.
(Comp. change caused by recruitm., temp. growth, etc.)
GROWTH
Senescent mort. coeff.
Fishing mort. coeff.
PREDATION
(First guess or previous time step)
BIOMASS (as adjusted with growth and mortalities)
MIGRATIONS (in DYNUMES only)
FEEDING (food consumption)
Food req. coeff. (as modif. e.g. by season)
Food composition (as modif. by availability)
PREDATION (CONSUMPTION) (by species)
Repeat above for all species
Sum predation of all species
Various time step outputs
Return to next time step computations
(At the end of the year adjust biomass in PROBUB)

FIG. 1. Schematic flow diagram of computations.

growth, the prescribed mean growth coefficient is adjusted (recomputed) at each grid point (and in each box in the PROBUB model) according to factors affecting it. This adjustment is done in each time step. The predation mortality is taken as the sum of the consumption of the given species (or group of species) in the previous time step (in first time step a guess is used, e.g. 7% of the biomass present). All other mortalities refer to actual time step. Using the computed growth and mortality rates, the actual biomass of each species is computed. In the DYNUMES model the migrations are computed thereafter, using prescribed u and v speed components. In the PROBUB model the migrations through the boundaries are adjusted empirically.

Before computing food uptake and actual composition of food, the availability of food items is checked at each grid point and adjustments are made, if necessary, to the composition of food. The consumption of each species during the time step is summed at the end of each time step.

A unique solution of a set of biomass and trophodynamic equations can be achieved if either the biomass of one major species is known (and kept constant during the iteration) or if part of the consumption (predation) is assumed to be known (e.g. consumption by mammals). In the iterative state of the PROBUB model the biomasses of the species must be adjusted at the end of each year (except of the species, the

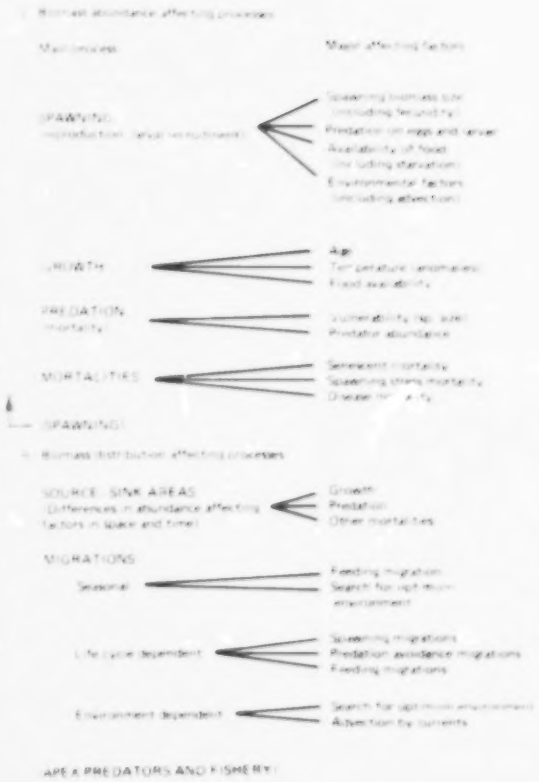

FIG. 2. Major dynamic processes in the marine ecosystem.

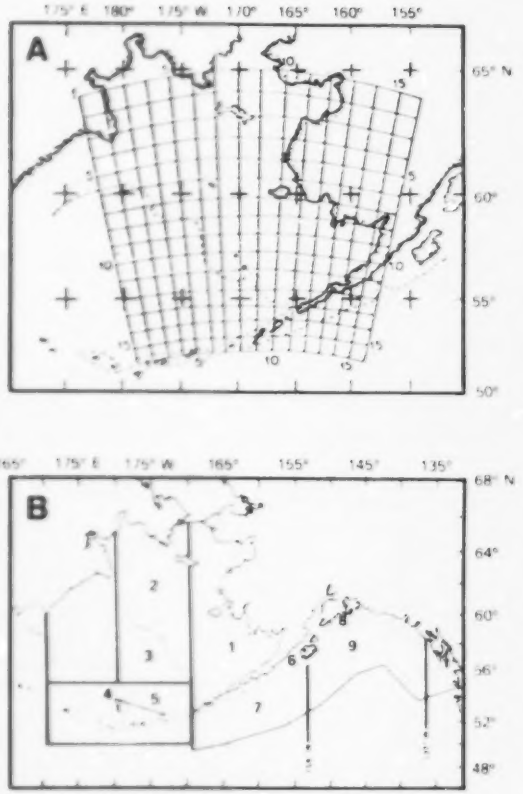

FIG. 3. Computation grid of DYNUMES for the eastern Bering Sea (A), and the computation areas ("boxes") for the PROBUB model (B).

biomass of which is assumed to be known). The PROBUB model provides the initial input of biomasses to the DYNUMES model.

The biomass-based model requires coefficients that are computed for biomass and for given time step length. A biomass growth coefficient is needed for the whole biomass. As this coefficient varies with age, a biomass distribution with age is required for its computation. The latter information is also used to estimate the portion of biomass which is vulnerable to predation (predator–prey size dependent predation). The computations of these biomass parameters are carried out in an auxiliary model (Laevastu and Favorite 1978c). An example of biomass distribution is given in Fig. 4.

Recruitment changes in the biomass model are reflected in the changes of growth coefficient, as the latter is a function of biomass distribution with age. The recruitment can thus be controlled with a parameter which is a function of equilibrium biomass and the actual biomass (i.e. high biomass results in proportionally lower recruitment and vice versa).

Evaluation of Resources in the Bering Sea and in the Gulf of Alaska with the PROBUB Model

Several applications of the bulk biomass model have been made in the northeastern Pacific for evaluation of the fishery resources (Laevastu and Favorite 1977, Laevastu et al. 1978). The latest updated bulk biomass model (i.e. PROBUB) was used to determine the equilibrium biomasses in the eastern Bering Sea and in the western Gulf of Alaska. An example of the results from the eastern Bering Sea is given in Table 1.

The consumption of fish, benthos, and plankton by marine mammals was computed with prescribed monthly amounts of mammals present and with fixed food composition. Thus consumption by marine mammals provided the "forcing function" which allowed the determination of the unique solution (i.e. the equilibrium biomasses). The basic principle of the determination of the equilibrium biomasses that can be sustained in a given ecosystem is that the annual biomass growth must equal its removal by predation, other mortalities, and the fishery. A preliminary numerical and theoretical evaluation of the accuracy of the determination of the equilibrium biomasses with the PROBUB model was done by introducing the plausible error limits in input data into the model computations. This evaluation indicated that the error is expected not to exceed ±30% of the computed mean equilibrium biomass of most exploited species. The greatest source of error was found to be caused by uncertainties in the food composition of major species.

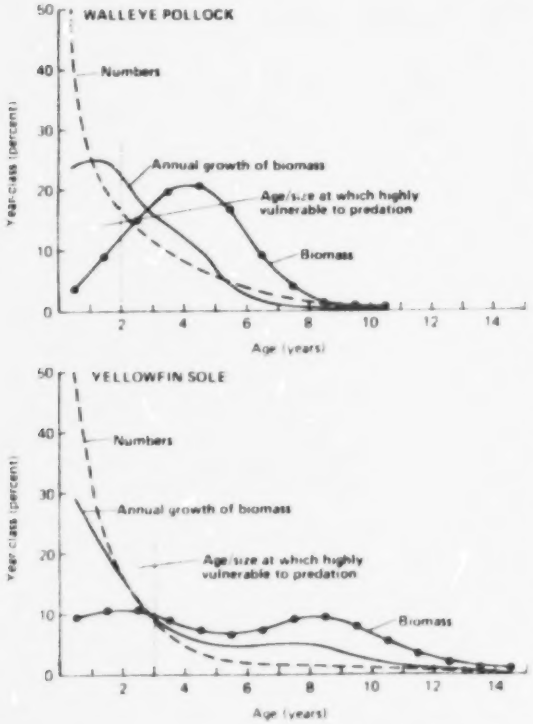

FIG. 4. Percentage of biomass, numbers, and annual growths in mean year-classes in walleye pollock and yellowfin sole in the eastern Bering Sea.

The equilibrium biomasses in the eastern Bering Sea (statistical and management areas 1, 2, and 3 (Fig. 3B)), given in Table 1, are the "minimum sustainable equilibrium biomasses" obtained by using the highest plausible growth rates and the lowest plausible food requirements and are grouped into three different ecological groups: pelagic, semidemersal, and demersal (Fig. 5). The semidemersal species dominate all other ecological groups (12 million t), mainly due to their more flexible feeding habits. The biomasses of pelagic and demersal species are about equal (about 7.5 million t each). The most abundant species is walleye pollock (about 9 million t), followed by cottids and other smaller, noncommercial demersal species (4 million t), and capelin (*Mallotus villosus*), other smelts, and sand lance (3.5 million t). Pacific salmon, which occur seasonally in the eastern Bering Sea, are not included in Table 1. The biomasses of the demersal species decrease more than one order of magnitude by moving from the continental shelf regime (area 1) to the deep ocean, mainly due to disappearance of the benthic food resource. The semidemersal species live a pelagic life and consume pelagic food over the deep water.

Very little is known about the benthos in the Bering Sea. The total equilibrium biomasses require about 50 g/m^2 standing stock of benthos. The existence of this standing stock is entirely possible if we compare the Bering Sea with the well-investigated Barents Sea.

Quantitative zooplankton data from the Bering Sea are nearly absent. The Soviet works in the early 1960s were quantitatively deficient, giving only the minimum standing stocks of copepods and no quantitative data on abundant euphausids. The total equilibrium biomasses consume about 50 g of zooplankton/m^2; thus annual production of zooplankton must be at least this amount. The exploitable biomasses in the western Gulf of Alaska as computed with PROBUB model and as ascertained with trawling surveys are given in Table 2.

The total exploitable finfish biomass (excluding capelin and cottids) over the continental shelf of the eastern Bering Sea is about 10 t/km^2 (capelin and cottid total biomass is about 7.5 t/km^2). Of this biomass only about 1.6 t/km^2 is taken by the fishery. Marine mammals consume in addition more than 3 t/km^2. Obviously many species are quite underexploited in the Bering Sea (flatfishes, capelin, Atka mackerel, etc.). Considering the relatively high consumption of fish by marine mammals and the relatively low commercial catch, it is very doubtful that the management of the fishery has any effect on the resources without simultaneous management of marine mammal herds. Furthermore, components of the marine ecosystem have long-term fluctuations which are not necessarily caused by the fishery.

The long-term dynamics of the biomasses in the marine ecosystem can be and have been studied with the PROBUB model after determination of the equilibrium biomasses by introducing a cause of any change in any species in the ecosystem. The results of such studies have limited reliability beyond a few years because of the uncertainty in predicting the recruitment (spawning success). It should, however, be pointed out that the "natural," quasi-periodic fluctuations of biomasses in the marine ecosystem can have considerable magnitudes (e.g. the biomass can be a fraction of a few tenths to several times its long-term mean value). The periods can be from a few years to more than a few decades.

Study of the Dynamics of Marine Ecosystem in Space and Time and its Effects on Resource Assessment

Two basically different causes for seasonal dynamics of biomasses can be recognized (i.e. changes in abundance and distributions in space and time). The first group of changes are caused by seasonally changing growth, predation (and other mortalities), and production and release of eggs and milt. The second cause of seasonal dynamics is seasonal migrations of species. The product (results) of both major causes of seasonal dynamics must be viewed spatially. Unfortunately little consideration has been given to the spatial aspects of biomass (and ecosystem) dynamics in the past, mainly due to difficulties in its empirical study by nonsynoptic resource surveys. However, the gridded ecosystem models with spatial resolution make these studies possible.

Examples of spatial and temporal aspects of biomass dynamics are shown in Fig. 6 which depicts the biomass sources and sinks in February and August of juvenile pollock (<22 cm long) in the eastern Bering Sea (source refers to the condition where biomass growth in a given time interval, month, exceeds its losses by predation, fishery and other

TABLE 1. Equilibrium biomasses and ecosystem internal consumption of some species or groups of species in the eastern Bering Sea (thousands of tonnes).

Species or groups of species	Total biomass, thousands of tonnes				% Exploitable biomass	Total exploitable biomass	Consumption, thousands of tonnes				Annual turnover rate
	Area 1	Area 2	Area 3	Eastern Bering Sea			Area 1	Area 2	Area 3	Eastern Bering Sea	
Halibut, turbot	260.5	142.1	8.8	411.3	54	222.1	66.9	31.7	2.8	101.4	0.25
Flatheai sole, arrowtooth flounder	945.1	236.4	17.0	698.4	54	377.1	147.7	69.6	7.0	224.3	0.32
Yellowfin sole, rock sole	661.8	444.7	24.0	1 130.5	45	508.7	174.1	87.6	9.2	270.9	0.24
Other flatfish	492.3	363.5	26.5	882.3	28	247.1	220.2	111.2	14.3	345.7	0.39
Cottids	2 478.1	1 450.0	189.5	4 117.6			1 347.2	664.7	115.8	2 127.7	0.52
Cods	593.9	391.5	50.6	1 036.0	72	745.9	301.2	168.6	31.5	502.3	0.48
Sablefish	71.3	37.7	18.0	127.0	40	50.8	18.6	10.2	1.4	30.2	0.24
Pollock	5 513.4	2 997.3	702.5	9 213.2	70	6 449.2	2 390.9	1 135.2	464.2	3 990.3	0.43
Rockfishes	1 089.9	477.3	139.0	1 626.3	30	487.9	445.2	210.9	65.8	721.9	0.44
Herring	1 219.1	578.5	171.4	1 968.9	30	590.7	832.9	399.1	125.6	1 357.6	0.69
Capelin, sand lance	2 165.8	1 047.8	292.3	3 505.8			1 550.7	749.5	219.2	2 519.4	0.72
Mackerel	701.3	330.4	131.9	1 163.6	45	523.6	387.9	183.0	78.3	649.2	0.56
Squid	523.3	248.4	498.3	1 270.1			621.5	307.5	668.1	1 597.1	1.26
Crab	522.2	309.9	14.3	846.4	40	338.6	180.0	93.1	5.9	279.0	0.33
Shrimp	427.3	479.9	24.3	931.5	65	605.5	350.0	187.8	14.2	552.0	0.59
Predatory benthos	466.6	378.0	41.7	886.3			198.0	138.4	20.8	357.2	0.40
Infauna	13 401.3	10 517.4	443.3	24 362.0			13 813.0	9 085.9	546.4	23 445.3	0.96
Epifauna	10 433.3	7 006.9	452.0	17 892.2			6 471.8	3 845.4	305.0	10 622.2	0.59

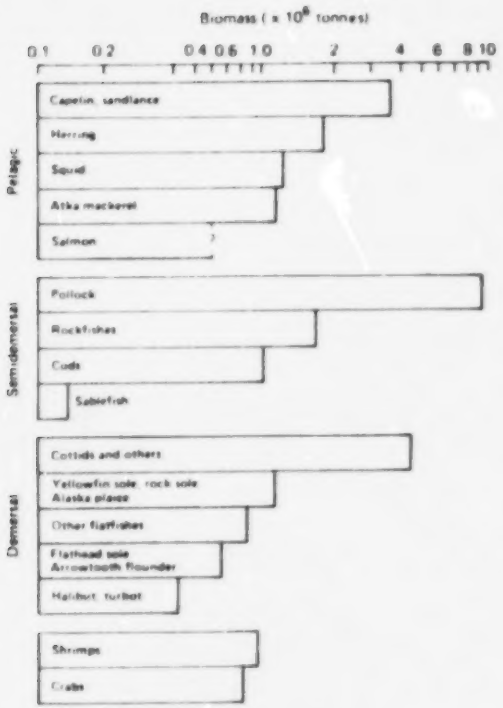

FIG. 8. Equilibrium biomasses of three ecologically different species groups in the eastern Bering Sea

mortalities; sink refers to opposite conditions (i.e. losses exceed growth)).

The sources and sinks of all species change in space and time due to spatial and temporal changes of the processes associated with them. There is usually a sink at the periphery of the distribution of the biomass. This sink is usually compensated by outmigration from the center of main distribution (spreading). There is a quasi-continuous source of walleye pollock off the continental slope over the deep water. During winter this source area is farther to the southwest where the temperature of the water is higher, allowing higher growth rates.

The distribution of the two different age-groups of walleye pollock in August is shown in Fig. 7. A partial separation of juvenile and old pollock is brought about by cannibalistic predation of old pollock on its own juveniles and other factors. The highest concentration of biomass of older pollock is found off the continental slope, whereas the juveniles are found mainly on the continental shelf.

The effects of seasonal depth migrations of yellowfin sole on changes in its distribution are shown in Fig. 8. The seasonal depth migrations of flatfish were investigated by Alverson et al. (1964). On the basis of this work it was assumed that yellowfin sole migrates from deep water into shallow water during May and June and back into deep water in October and November. A migration speed of 3 km/d was assumed in the model. The distribution of yellowfin sole in August is given in Fig. 9 as computed with the DYNUMES model.

The seasonal migrations have profound effects on other biota as well as on the evaluation of fishery resources with trawling surveys. For example, the flatfish is dependent on

TABLE 2. Comparison of exploitable biomasses (thousands of tonnes) as obtained by surveys and computed with PROBUB model. Western Gulf of Alaska.

Species or group of species	1970s mean from surveys[1]	Minimum sustainable exploitable biomass from PROBUB model
Demersal		
Greenland turbot, halibut	138	52
Flathead sole, arrowtooth flounder	77	50
Yellowfin and rock sole, Alaska plaice	78	80
Other flatfish	30	42
Elasmobranches, cottids	86	(493)
Semidemersal		
Walleye pollock	1024	1228
Pacific cod	112	101
Sablefish	13	(20)
Rockfish	25	134
Pelagic		
Pacific herring		129
Capelin, other smelt		(500)
Varia		
Atka mackerel + macrurids		168
Squid		(680)
Crab	213	58
Shrimp		121

[1] Survey results for 1970s from Ronholt et al. (1978). Converted with catchability coefficient

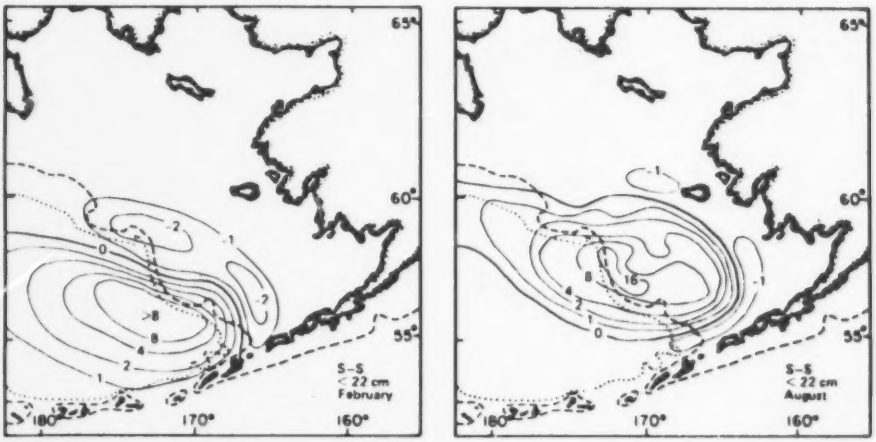

FIG. 6. Sources and sinks of juvenile walleye pollock (< 22 cm long) in February and in August in the eastern Bering Sea (in 100 kg/km²).

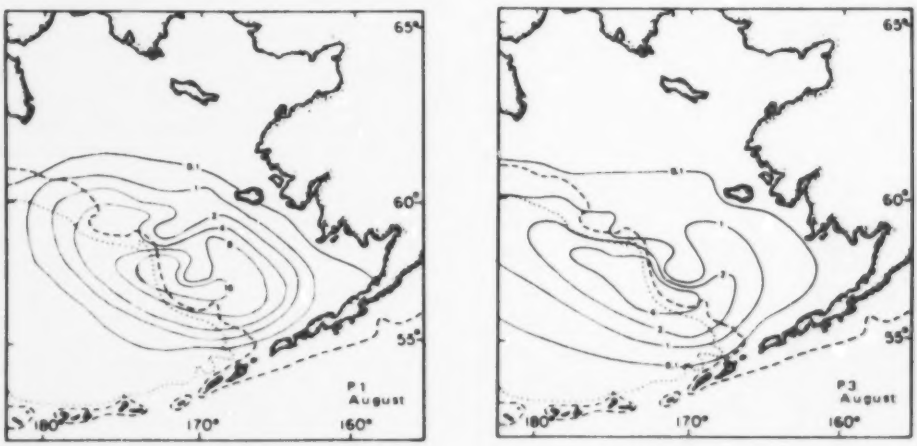

FIG. 7. Distribution of juvenile walleye pollock (< 22 cm long) and old walleye pollock (> 45 cm long) in August in the eastern Bering Sea (t/km²).

benthos as a food source. The migrations cause heavy grazing of benthos in some areas during some seasons, allowing "recovery period" during other seasons. A proper trawling survey evaluation must account for seasonal migration to avoid meaningless results.

Two dynamic effects of temperature anomalies are included in the DYNUMES model: the "forced" migration of most species out from areas with subzero bottom temperatures in the Bering Sea (including a slightly increased mortality), and the effect of temperature on growth (and food uptake).

An example of the resulting effect of temperature anomalies on the growth of herring biomass is given in Fig. 10, showing the sources and sinks of biomass in an average February and in a February with 1.5°C positive temperature anomaly. The growth of biomass is considerably enhanced in the February with the positive temperature anomaly, especially in the southern, warmer part of the Bering Sea. The effects of cold anomalies on growth are less than the effects of warm anomalies, as the growth is nearly arrested at low temperatures.

Verification of the Model and Validation of the Results

The verification of the ecosystem simulation models has been done by testing that the formulas used in the models reproduce known effects and behaviors for which they are designed. Furthermore, the verification has been done by simulating events with the models that are known to produce

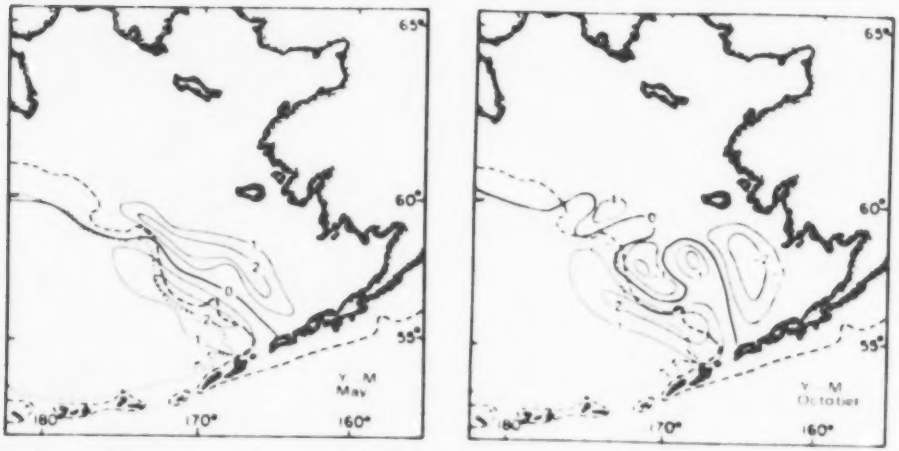

FIG. 8. Changes of yellowfin sole biomass distribution due to migrations in May and in October (t/km²).

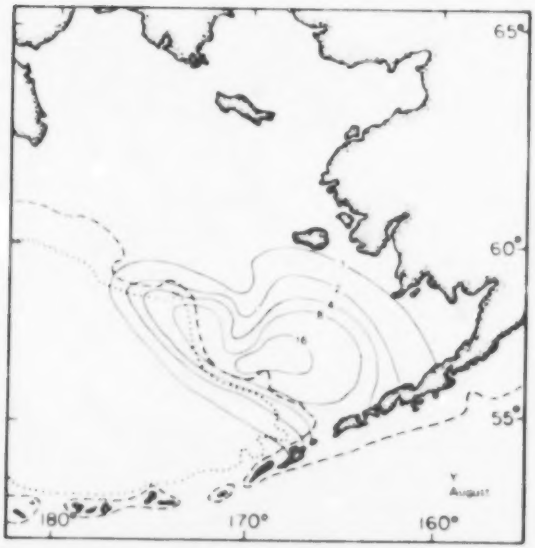

FIG. 9. Distribution of yellowfin sole in August in the eastern Bering Sea (t/km²).

given changes in the ecosystem. Thus the sensitivity study in large ecosystem models becomes a continuing study of the response of the ecosystem to changes in various rate and state parameters.

The validation of the ecosystem model is done by comparing the resulting state variables (e.g. the abundance and distribution of biomasses) with independently obtained empirical data (e.g. from fisheries surveys). The dynamic aspects of the Bering Sea ecosystem are, however, difficult to validate empirically, due to the absence of time series studies. Before validating the model results with available resource survey results, the latter must be properly converted using catchability coefficients. Examples of this validation are given in Tables 2 and 3 for the species that are more reliably reported quantitatively in the resource surveys. In general, the resource surveys are accurate only to about ± 50% (Grosslein 1976), whereas the preliminary estimation of the error in the model computation indicates that the error in these results does not exceed ± 30% of the reported value for major species.

Some special qualitative validation of the simulation models can be provided by occasional special fisheries surveys. The following serves as an example. In the early stage of the Bering Sea ecosystem modeling, it became obvious that there must be a considerable amount of walleye pollock (and some

TABLE 3. Comparison of exploitable biomasses of some species as obtained by surveys and as computed with PROBUB model. Eastern Bering Sea. (Thousands of tonnes.)

Species or group of species	Mean 1975, 1976 surveys (converted) from Bakkala and Smith (1978)	Equilibrium exploitable biomass from PROBUB model	Catch 1975
Greenland turbot, halibut	176	222	65
Flathead sole, arrowtooth flounder	206	377	26
Yellowfin and rock sole, Alaska plaice	2716	509	74
Walleye pollock	3698	6449	1285
Pacific cod	233	746	57

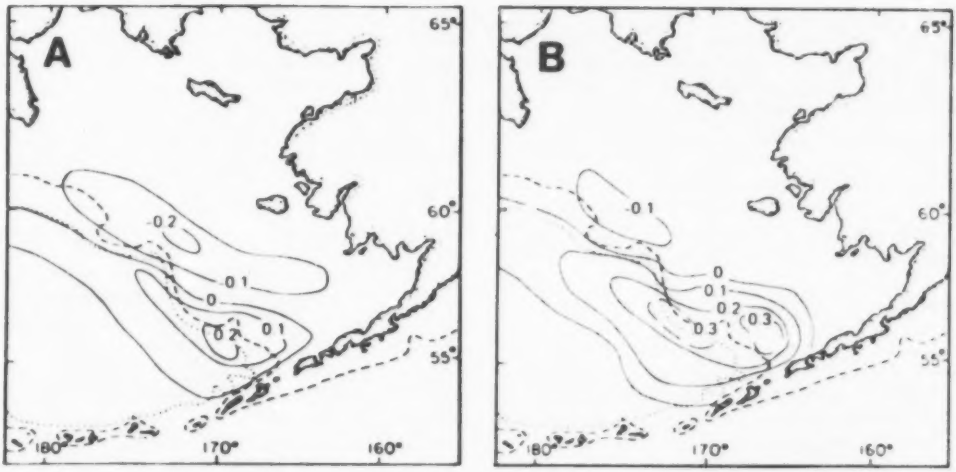

FIG. 10.—Effect of temperature anomaly on the source and sink of Pacific herring in February in the eastern Bering Sea (A, "normal" February; B, February with a +1.5°C temperature anomaly).

other fish species) over the deep water in the Bering Sea. However, walleye pollock were never caught over deep water and the model results were severely criticized until a recent Japanese survey showed considerable amounts of older (larger) pollock over deep water. Furthermore, the deep water areas turned out to be source areas of biomass for many pelagic and sempelagic species at least part of the year. The abundant euphausids in this area provide ample food source. However, no extensive schooling occurs over deep water, making the fishery less profitable there than over the continental shelf.

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Appendix

Skeleton Bulk Biomass Model

The skeleton bulk biomass model (SKEBUB) derived from the bulk biomass model (BBM) of Laevastu and Favorite (1978a) was to a great extent written by Dr Niels Daan from the Netherlands Institute for Fisheries Research during an ecosystem model workshop in Seattle. It is the simplest multispecies ecosystem model based on biomass (in contrast with conventional number-based models). One of the purposes of this model is to explain the essentials of fisheries ecosystem simulation.

The equations presented here can be applied to any fish species. The formulations and treatment of plankton and mammals (apex predators) are excluded. The biomass and trophodynamic equations can also be applied, with some modifications, to single cohort of any species. The numerical behavior of the individual formulas is well-known and thus

not described here.

The biomass growth and mortality is computed in discrete time steps. The biomass growth rate is computed from empirical data of annual growth rates and distribution of biomass with age. The latter is computed with an auxiliary model (Laevastu and Favorite 1978b).

The biomass (B) of a cohort, species, or group of species (i) at the end of a given time step (t) (monthly time step is normally used) is computed with a well-known formula (1), using biomass from previous time step ($t-1$) and growth rate (coefficient) (g) minus total mortality rate (Z) for this time step.

$$(1) \quad B_{i,t} = B_{i,t-1} * e^{(g_{i,t} - Z_{i,t})}$$

The yield (Y) is computed with a prescribed fishing mortality coefficient ϕ_i. It should be noted that all the instantaneous coefficients (growth, mortality, fishery) are different than the corresponding conventional coefficient for number-based models which use annual time step. Thus all these coefficients have to be computed on biomass base and for the time step used in the model.

$$(2) \quad Y_{i,t} = B_{i,t} - B_{i,t} * e^{-\phi_{i,t}}$$

As a relatively short time step is used in the computation, the second-order terms, such as nonlinearities in growth and mortality during the time step, can be neglected.

The growth coefficient is computed in each time step, accounting for the effects of starvation in previous time step.

$$(3) \quad g_{i,t} = g_i'' * ((R_{i,t-1} - S_{i,t-1})/R_{i,t-1})$$

If there was no starvation in the previous time step ($S_{i,t-1} = 0$), the rate of growth ($g_{i,t}$) will take the prescribed value g_i'', but if the species was not able to get all the food required ($R_{i,t}$) for maximum growth rate, the prescribed growth rate will be reduced by the ratio of the amount of food which the species was not able to get during the previous time step ($R_{i,t-1} - S_{i,t-1}$) over the total amount of food required by the biomass to grow under unlimited conditions ($R_{i,t-1}$). Both values are available from the previous time step and the possible error caused by this necessary backstepping choice is again minimized by the use of a short time step in the computations.

The initial (prescribed) growth rate can be presented as a harmonic function over time to take account of seasonal differences in growth ($g_i'' = \gamma_i + \sigma_i * \cos(\alpha_i t - \kappa_i)$) where γ_i is the annual mean growth coefficient, σ_i is half of the magnitude of its annual change, α_i is the phase speed, and κ_i is the time lag to reach the maximum. Furthermore, in full BBM models the growth rate is made a function of either surface or bottom temperature. Growth rate is also a recruitment parameter in biomass-based models (see below).

The mortality rate ($Z_{i,t}$) is the addition of all negative rates of changes representing thus the total mortality rate:

$$(4) \quad Z_{i,t} = \phi_{i,t} + \mu_i + \beta_{i,t}$$

All rates of change are presented as instantaneous coefficients and are therefore additive. Fishing mortality ($\phi_{i,t}$) and natural mortality from old age and diseases, including also spawning stress mortality (μ_i), are prescribed, but the predation mortality coefficient ($\beta_{i,t}$) is computed trophodynamically in previous time step from the ratio of consumption of the species over its biomass ($\beta_{i,t} = \ln(1 - (C_{i,t-1}/B_{i,t-1}))$).

The amount of food eaten by a species ($R_{i,t}$) with unlimited food availability is:

$$(5) \quad R_{i,t} = B_{i,t} * r_i * \tau$$

where r_i is the prescribed daily ration (in fraction of body weight daily) and τ is the length of time step in days. If the growth rate (g_i'') is made a harmonic function over the year, r_i must also be made a harmonic function ($r_i = \rho_i + \delta_i * \cos(\alpha_i t - \kappa_i)$).

If the food supply of all food items for a given species would be unlimited, we could compute the consumption of each food item (e.g. the consumption of species j by species i (C_{ij})) from the food requirement (R_i) and the fraction of species j (prey) in the food of species i (predator) (π_{ij}):

$$(6) \quad C_{ij} = R_i * \pi_{ij}$$

In this case the total consumption of species i would be:

$$(7) \quad C_i = \sum_j C_{ij}$$

and the starvation would be 0. However, some food might be in limited supply and only part of the biomass of a prey is usually accessible as suitable food (re size-dependent feeding). The vulnerability of one species (prey) to another species (predator) is prescribed by average composition of the food of predator. Therefore the fraction of each species that is allowed to be consumed in each time step is prescribed in the model (p_{ij}), considering mainly the size composition of the biomasses of individual species. Furthermore, substitution of low-availability food items with high-availability items must be used. However, conditions can arise where full substitution is unrealistic and partial starvation will occur. There are various ways of computing the actual consumption with above described limitations.

The recruitment is usually depicted in number-based models as a discontinuity relating it to discrete spawning period. In our biomass-based model we have treated it as a continuous process. This treatment is acceptable if we think in terms of size-groups rather than age-groups and consider variations in growth of individuals belonging otherwise into the same age-groups, and assume a longer spawning period, as is the case with most species.

Considering a continuous recruitment to all size-groups and assuming that there are no exceptionally strong or weak year-classes of postlarval juveniles, the recruitment would be proportional to the biomass present. The variations in postlarval recruitment would be depicted in the biomass-based model by the variations of growth coefficient of the species biomass.

On the other hand, large spawning biomasses are known to produce proportionally smaller year-classes and small spawning biomasses are known to produce proportionally large recruitment (year-classes). Therefore, the recruitment could be regulated (controlled) in biomass-based models, making the growth coefficient inversely proportional to biomass

present.

$$g_i^0 = g_i^0 B_i^e / B_{i,1}$$

where B_i^e is the equilibrium or mean biomass of species i. This computation can be done in the models in prognostic mode after the determination of the equilibrium biomasses.

If the biomasses of all species in the ecosystem do not change over a year (i.e. previous January biomass is the same as actual January biomass), then we can say that the biomasses are in equilibrium. This implies that the growth of the biomass equals its removal by mortalities (specially by predation). If we want to achieve this equilibrium, we can change either growth rate, mortality rate, or biomass level itself. The growth rate is determined by empirical data and the other factors, such as temperature, are assumed in equilibrium case to be the same from one year to another (although seasonal changes can occur). Fishing and other mortality rates are also assumed to remain the same from one year to another. The predation mortality (consumption) (together with other mortalities that remain unchanged) must then balance the growth rate. This balancing can be achieved if the biomass levels of the predators are adjusted so that the biomasses remain constant from one January to another January. This adjustment can be done by finding a unique solution to the biomass equations of all species (or groups of species) in the ecosystem. This unique solution exists when one of the biomasses and consumption by it is predetermined (assumed to be known and fixed). In this case an iterative solution can be applied to adjust the biomasses of other species once after each year's computation:

$$B_{i,12,n} = B_{i,12,n-1} + \frac{(B_{i,0} - B_{i,n})}{k}$$

where $B_{i,12,n}$ is the new (adjusted) biomass for December, $B_{i,12,n-1}$ is the previous December biomass, $B_{i,0}$ is the biomass of previous January (computed as next step from $B_{i,12,n}$), $B_{i,n}$ is the computed biomass in January 1 yr later, and k is an iteration constant (2.5 to 10, depending on the state of convergence). Forty years or more of computation is needed before the solution converges to a unique (equilibrium) solution.

The model requires as input a number of species specific constants. Besides these, the biomass of at least one species must be prescribed as known (i.e. not altered in iterative adjustment). The biomasses of other species must be initially prescribed as the best first guesses. The first guess values of the consumption (C) can be computed by assuming C_i to be seven percent of B_i per month.

To determine the carrying capacities of given ocean regions with the model and to obtain realistic equilibrium biomasses, the model must include all species. Computer capacity as well as basic information available does not usually allow the specification of all species separately, but many species must be grouped into ecological groups, whereby the composition of food and feeding habits are the main criteria for grouping.

Symbols for Constants, Calculated Variables, and State Vectors

Constants

- α_i Phase speed, time step dependent (e.g. 30° per month, radians)
- β_i Predation mortality
- γ_i Annual average instantaneous growth rate
- ϕ_i Instantaneous fishing mortality coefficient
- ∂_i Half amplitude of annual change of food requirement (fraction of body weight daily)
- σ_i Half amplitude of annual change of growth rate
- ρ_i Annual average food requirement (fraction of body weight daily)
- κ_i Phase lag (in radians)
- μ_i Instantaneous rate of mortality (other than predation mortality, including spawning stress mortality)
- $\pi_{i,j}$ Fraction composition of prey j in the food of predator i
- p_i Fraction of biomass j allowed to be taken in one time step (month)
- r_i Prescribed ration (food requirement, fraction of body weight daily)
- g_i^0 Prescribed instantaneous growth rate

Note: The latter two parameters (r_i and g_i^0) can also be computed if γ_i and ρ_i and related constants are prescribed.

Dynamically calculated parameters

- $g_{n,i}$ Calculated instantaneous growth rate
- $Z_{n,i}$ Calculated total instantaneous total mortality rate
- B_i^e Equilibrium biomass

State vectors

- $B_{t,i}$ Biomass of species i at time t
- $C_{n,i}$ Consumption of species i (predation) during time step t
- $C_{i,j}$ Consumption of species j by predator i
- $R_{n,i}$ Food requirements
- $S_{n,i}$ Starvation (the amount of food missing from the full food requirement ($R_{n,i}$)
- $Y_{n,i}$ Yield

Empirical Examination of Population Interactions for the Fishery Resources off the Northeastern USA

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Sissenwine, M. P., B. E. Brown, J. E. Palmer, R. J. Essig, and W. Smith. 1982. Empirical examination of population interactions for the fishery resources off the northeastern USA. p. 82–94. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

The Gause competition model (modified to account for fishing) was fit for 724 combinations of population units of the Georges Bank and southern New England area. The population interaction coefficient of the model for 4% of the combination was statistically significant at the 5% level. The model was also modified to include a time-lag effect to reflect better the assumed impact of predation of young fish. This model was applied to 198 combinations of population units (with the lagged term always representing assumed predators). For the lag model, 5% of the interaction coefficients were significant at the 5% level. Thus, many (if not all) of the significant interaction coefficients may result from type I errors, i.e. no valid evidence of population interactions was obtained.

The inability to demonstrate empirically significant population interactions may result from inadequate data bases describing the populations, an inadequate population model, and or colinearity of variables used to fit the model. It is also possible that productivity of particular populations of the region is not significantly related to abundance of other populations.

One shortcoming of the Gause competition model is that it fails to describe the role of recruitment in population dynamics. Therefore, the interrelationship between "strong" year-classes of 10 species of Georges Bank was considered qualitatively. The results indicate that strong year-classes of fish predators (silver hake, cod) and prey species (sand lance, squid) do not co-occur.

Key words: population interactions, multispecies fishery models, competition, predator–prey.

Sissenwine, M. P., B. E. Brown, J. E. Palmer, R. J. Essig, and W. Smith. 1982. Empirical examination of population interactions for the fishery resources off the northeastern USA. p. 82–94. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

Le modèle de compétition de Gause (modifié pour tenir compte de la pêche) peut s'appliquer à 724 combinaisons d'unités de populations du banc Georges et du sud de la Nouvelle-Angleterre. Pour 4 % de ces combinaisons, le coefficient d'interaction des populations du modèle est significatif à l'analyse statistique au niveau de 5 %. Le modèle a également été modifié de façon à inclure un effet de décalage qui refléterait mieux l'impact présumé de la prédation sur les jeunes poissons. Ce modèle a été appliqué à 198 combinaisons d'unités de populations (le terme de déclage représentant toujours les prédateurs présumés). Avec ce modèle 5 % des coefficients d'interactions sont significatifs au niveau de 5 %. Il se peut donc que plusieurs (si non tous) coefficients d'interaction significatifs résultent d'erreurs de type I, c.-à-d. qu'on ne peut s'assurer qu'il y ait interactions entre populations.

Cet échec peut résulter de données impuissantes à décrire les populations, d'un modèle de populations inadéquat et (ou) de la colinéarité des variables utilisées dans l'application du modèle. Il se peut aussi qu'il n'y ait pas de relation entre la productivité de populations particulières de la région et l'abondance d'autres populations.

Le modèle de compétition de Gause a le défaut de ne pouvoir décrire le rôle du recrutement dans la dynamique des populations. C'est pourquoi la relation entre les « fortes » classes d'âge de 10 espèces du banc Georges a été étudiée qualitativement. Les résultats indiquent qu'il n'y a pas cooccurrence d'une abondante classe d'âge de poissons prédateurs (merlu argenté, morue) et d'espèces proies (lançon, encornet).

Introduction

The need for multispecies management is a recurring theme of numerous scientific papers (Hennemuth 1977; Larkin 1977; Sissenwine 1978; May et al. 1979; Gulland 1978), meetings, and the deliberation of international commissions dealing with fisheries management (International Commission for Northwest Atlantic Fisheries, ICNAF; and the International Council for Exploration of the Sea, ICES). Although the existence of fishery (by-catch) and biological (predator–prey or competition) interactions is undeniable, quantitative methods suitable for analysis of the latter at the

population level are necessary.

Both complicated process oriented ecosystem models (Anderson and Ursin 1977; Laevastu and Favorite 1976) and simpler heuristic models (May et al. 1979; Horwood 1976; Pope 1976) have been described in the scientific literature. Process oriented ecosystem models are usually fishery specific and data hungry with limited predictive capability. Such models are useful as research tools aimed at the development of general principles concerning the dynamics of fishery systems. On the other hand, heuristic models may provide an empirical basis for the management of interacting fish populations. This possibility, for the offshore fishery resources of the northeastern USA, is considered here.

Data Base and Method of Analysis

Gause (1934) competition equations are an obvious extension of the Verhulst–Pearl logistic equation (Pielou 1977). Similarly, the Schaefer (1954, 1957) model is logically extended to two species as follows:

$$(1)\quad \frac{1}{P_i}\frac{dP_i}{dt} = a_i - b_iP_i - F_i \pm c_{ij}P_j$$

where P_i is an instantaneous measure proportional to population size, F_i is an instantaneous measure of fishing mortality rate, a_i, b_i, and c_{ij} are parameters, and $i = 1,2$, $j = 1,2$, $i \neq j$ (Pope 1976). The parameter c_{ij} is negative when P_j is a competitor or prey of P_i and it is positive when P_j is a predator of P_i. Because the instantaneous catch rate (C_i) is proportional to $F_i \cdot P_i$, equation (1) may be written as:

$$(2)\quad \frac{1}{P_i}\frac{dP_i}{dt} = a_i - b_iP_i - q_i\frac{C_i}{P_i} \pm c_{ij}P_j$$

where q_i is the coefficient of proportionality between P_i and actual population size. The following approximations are used to express equation (2) in a form amenable to multiple linear regression:

$$(3)\quad \frac{dP_i}{dt} \approx P_{i,k} - P_{i,k-1}$$

$$(4)\quad P_i \approx \frac{P_{i,k-1} + P_{i,k}}{2} = X_i$$

$$(5)\quad C_i \approx \bar{C}_{i,k}$$

$$(6)\quad \frac{1}{P_i}\frac{dP_i}{dt} \approx \frac{P_{i,k} - P_{i,k-1}}{X_i} = Y_i$$

$$(7)\quad \frac{C_i}{P_i} \approx \frac{\bar{C}_{i,k}}{X_i} = Z_i$$

for $k = 1,2,\ldots,n$ where the second subscript is used to indicate the sequence of evenly spaced observations and $\bar{C}_i$ is the average catch rate (or total catch during a unit time interval) during the time interval between observations. Thus parameters a_i, b_i, q_i, and c_{ij} are estimated by fitting the multiple linear regression to data where Y_i is the dependent variable and X_i, Z_i, and X_j are independent variables. The partial correlation coefficient for c_{ij} is calculated for each regression to judge the significance of empirical evidence of an interaction between species i and j.

Obviously, the multiple linear regression approach to fitting the parameters of equation (2) only approximates the actual continuous differential equation model. An alternative method of estimating the model parameters is available.

Equation (2) may be rewritten as

$$(8)\quad \frac{d(\log_e P_i)}{dt} = a_i - b_iP_i - q_i\frac{C_i}{P_i} \pm c_{ij}P_j$$

because by application of the chain rule of calculus, $d(\log_e X(t))/dt = (1/X(t)) \cdot dX(t)/dt$. This differential equation can be numerically integrated to simulate the model with parameters adjusted iteratively until a least-squares solution is obtained. The method used here is based on a rather complex extension of a standard nonlinear least-squares fitting method (Box 1960; Marquardt 1963). A general purpose computer program capable of fitting differential equations to data was developed. The program is similar to those developed by Berman and Weiss (1978) and Metzler et al. (1974).

Unlike fits of the linearized version of the model, local minima in sums of squares exist when the nonlinear method is used to fit equation (8). Therefore, care must be exercised in interpreting results. Several sets of initial parameter estimates (used to start the fitting procedure) should be considered. If initial parameter estimates are not realistic, the method may fail to converge to a minimum of sums of squares. Thus, the nonlinear method was only applied to a small subset of the population combinations for which the linearized version of the model was fit.

Application of the model described by equations (2) and (8) requires some measure of population size and of catch. Since 1963, standardized research vessel bottom trawl surveys have been conducted in the autumn of each year along the northeast coast of the USA from just south of Hudson Canyon to Nova Scotia and from a depth of about 27 m to the edge of the continental shelf (Grosslein 1969; Clark 1979). In 1967, the survey area was extended southward to Cape Hatteras. A standard "36 Yankee" trawl with a 1.25-cm stretch-mesh codend lining has been used throughout the time series of autumn surveys. The trawl measures 24 m along the footrope, averages 3 m in height along the headrope, and is equipped with rollers to make it suitable for use on rough bottom.

Sampling has been based on a stratified random design; the survey area has been stratified into zones based on depth and latitude (Fig. 1). As noted earlier, only strata 1–42 were sampled prior to 1967.

Approximately 300 stations are sampled during each survey although in recent years this number has sometimes been nearly doubled. Stations are allocated to strata approximately in proportion to the area of each stratum with specific assignment within strata on a random basis. A 30-min tow at an average speed of 3.5 knots is made at each station. The catch from each tow is sorted to species and the number, weight,

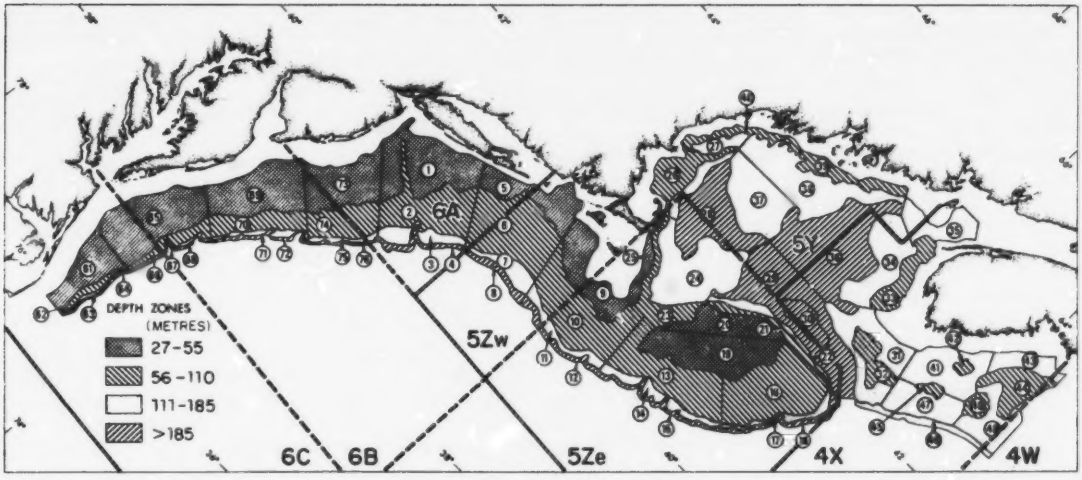

FIG. 1. USA research vessel bottom trawl survey strata definition.

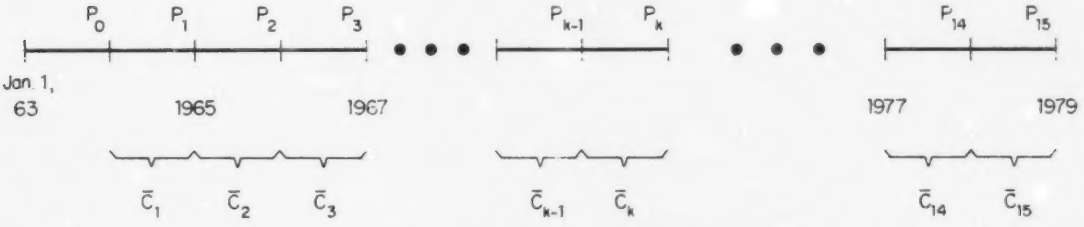

FIG. 2. Diagram of sequence of data used in linear regressions. P_k represents a measure of abundance based on the autumn research vessel bottom trawl survey of year 1963 + k. $\bar{C}_k$ is the total catch during year 1963 + k.

and length frequency determined and recorded; material for age and maturity stage determinations and for gut content analysis and other information is also collected as required. All data are stored, and processing is handled by a data management system. Thus, for those species vulnerable to the sampling gear, a considerable time series of data is available as a measure of population size ($P_{i,k}$, where i indicates species and k indicates time).

Results of autumn surveys are more representative of population size ~2 mo later at the beginning of the next year than at the beginning of the year of the survey. Therefore, the survey data from the autumn of year k and $k-1$ are used to represent the rate of change and average size of the population in year k as diagrammed in Fig. 2. Catch data are taken directly from the statistical bulletins of ICNAF or various stock assessment documents prepared by the Northeast Fisheries Center, Woods Hole. In some cases, catch during the early 1960s had to be estimated by prorating data from a later period to finer areal breakdown to accommodate the desired population definitions.

The fishery resources of the northeastern USA were grouped for analyses in a manner consistent with current management units and/or ecological considerations. Two important faunal areas were considered: Georges Bank (G.B., Strata 13–25, generally conforming to ICNAF SA 5Ze) and southern New England (S.N.E., 1–12, generally conforming to ICNAF SA 5Zw+6a). In some cases these were combined (indicated by C). The following populations or population groups were analyzed: silver hake (*Merluccius bilinearis*), G.B., S.N.E., C; red hake (*Urophycis chuss*), G.B., S.N.E., C; Atlantic cod (*Gadus morhua*), C; haddock (*Melanogrammus aeglefinus*), G.B.; pollock (*Pollachius virens*), C with Gulf of Maine; yellowtail flounder (*Limanda ferruginiea*), G.B., S.N.E.; winter flounder (*Pseudopleuronectes americanus*), C; summer flounder (*Paralichthys dentatus*), S.N.E.; total flounder (all species), C; butterfish (*Peprilus triacanthus*), C; river herring (*Alosa pseudoharengus* and *Alosa aestivalis*), C; shortfinned squid (*Illex illecebrosus*), C; longfinned squid (*Loligo pealei*), C; squid, C; dogfish (all species), C; bluefish (*Pomatomus saltatrix*), C; scup (*Stenotomus chrysops*), C; total finfish and squid (excluding menhaden, other primarily coastal species, and large pelagics), C.

The stratified mean catch in weight per tow for each population over the appropriate strata set was calculated for each survey and assumed proportional to population size. There is evidence supporting the assumption that research vessel bottom trawl survey results generally track trends in population

abundance, e.g. survey results are correlated with commercial catch per unit effort for yellowtail flounder, survey results are correlated with haddock VPA results, and increased survey catches of squid paralleled the development of a commercial fishery. Clark (1979) provides further support for this assumption. The precision of survey results was investigated by Grosslein (1971) and Pennington and Grosslein (1978). These papers indicate the coefficient of variation of stratified mean catch per tow is generally about 25%.

For some stocks, the results of virtual population analysis (VPA) are available as a measure of population size. This is particularly important for pelagic species like Atlantic mackerel (*Scomber scombrus*) and Atlantic herring (*Clupea harengus harengus*) for which bottom trawl survey data were not considered. Results of VPA were considered for mackerel from Cape Hatteras to the Gulf of St. Lawrence, herring from Georges Bank and southern New England combined, and silver hake, cod, and haddock from Georges Bank. Further details of the source of data for each of the population units noted above are given in Table 1.

The linearized version of equation (2) was fit to data for all logical combinations of population units. That is, an interaction between Georges Bank silver hake and southern New England red hake was considered illogical, although an interaction between these populations within either area is logical. In addition, the nonlinear fitting procedure discussed above was applied to equation (8) for two sets of data to determine the sensitivity of the results to the analytical method employed.

In the case of predation, the abundance of the prey population may be more closely related to predator abundance some time earlier rather than concurrently. This occurs when predatory species feed primarily on young fish (of another species) which are not yet a significant component of the biomass. The survival or mortality (partially from predation) of these young fish determines the future size of the prey population. Therefore, the linearized version of equation (2) was fit with measures of predator population size lagged by 1 yr. The introduction of a time lag reduces the number of paired observations of abundance and degrees of freedom of the analysis. Therefore, consideration was limited to a time lag of 1 yr. Furthermore, most of the species considered recruit to the survey and commercial catch at age 1 and 2, respectively; thus a short lag time is appropriate. The lagged predator populations considered (as independent variables) were silver hake (Georges Bank, southern New England, and Georges Bank VPA), cod (southern New England and Georges Bank combined, and VPA for same area), dogfish (southern New England and Georges Bank combined), and bluefish (southern New England and Georges Bank combined).

In addition to the quantitative method of analysis of population interactions discussed above, the interrelationship between recruitment or reproductive success of populations was also considered qualitatively. For many fisheries, productivity depends on the occurrence of large year-classes. Therefore, a logical approach to the examination of population interactions is consideration of the co-occurrence or lack thereof of "strong" year-classes. For the purpose of this discussion, a strong year-class is defined as a year-class larger than the size of the 75th percentile of all measured year-classes or a year-class larger than those occurring in adjacent years ($R_t > R_{t-1}$ and $R_t > R_{t+1}$, for VPA data only as noted below). Accordingly, some small year-classes will be defined as strong during extended periods of poor recruitment (e.g. haddock during the late 1960s and early 1970s, yellowtail flounder during the 1970s). The implication of describing small year-classes as strong based on their size relative to adjacent year-classes is that when recruitment is generally poor because of environmental conditions (biotic and abiotic including fishing), relative peaks in year-class size may be associated with a particular interacting species.

Trends in recruitment were examined for Georges Bank cod, haddock, silver hake, red hake, yellowtail flounder, mackerel, herring, and sand lance (*Ammodytes americanus*), shortfinned squid and longfinned squid. Sand lance recruitment was based on both research vessel bottom trawl surveys and larval surveys (Smith et al. 1978; K. Sherman, NEFC, Narragansett Laboratory, personal communications), squid recruitment was based on trawl surveys, and recruitment of the remaining species was based on VPA except for the most recent 3 yr that also were based on trawl surveys. The data base is described in greater detail by Hennemuth et al. (1980). Where survey data were used, only year-classes larger in size than the 75th percentile were considered as strong since sampling variation may result in spurious peaks.

Results and Discussion

The linearized version of equation (2) was fitted to data for 926 logical combinations of population measures. For 198 of these equations, the assumed predator abundance (independent variable) was lagged by 1 yr. The estimated parameters generally had the correct sign (a_i should be +, b_i and q_i should be −). Where the signs of parameter estimates were not consistent with the model, they were not significantly different from zero. In fact, the Schaefer model alone ($c_{ij} = 0$) commonly failed to explain a significant proportion of the variability in measures of population size.

The partial correlation coefficients (PCC) for the interaction between combinations of the 29 measures of population size without time lags are given in Table 2. Negative values of PCC indicate competition or that the population used as an independent variable (displayed horizontally) is a predator of the population modeled by equation (2). Positive values of PCC indicate that the modeled population (displayed vertically) is a predator of the population used as an independent variable.

Twenty-six of the values of PCC are statistically significant at the 5% level. Many of these apparent interactions seem unlikely on biological grounds. Total flounder (G.B. + S.N.E.) predation on pollock, competition between longfinned squid (G.B. + S.N.E.) and winter flounder (G.B.), and scup (G.B. and S.N.E.) as an important prey (affecting total productivity) of the total finfish and squid population (G.B. and S.N.E.) are examples of statistically significant interactions that seem unlikely. On the other hand, a significant negative interaction between silver hake (VPA) and haddock (VPA or survey measure) on Georges Bank, between cod (VPA, G.B. + S.N.E.) and total flounder

TABLE 1. Source of catch data and population measures.

	Population unit	Survey population measure	Catch
1.	Silver hake G.B.	1963–74 Clark and Brown (1977) 1975–78 unpublished data	1963–77 Almeida and Anderson (1979a) 1978 ICNAF Summ. Doc. 79/VI/30
2.	Silver hake S.N.E.	1963–74 Clark and Brown (1977) 1975–78 Almeida and Anderson (1979b) 1978 unpublished data	1963–77 Almeida and Anderson (1979b) 1978 Almeida (personal communication)[a]
3.	Silver hake G.B. and S.N.E.	1963–74 calculated from Clark and Brown (1977) 1975–78 unpublished data	1963–77 calculated from Almeida and Anderson (1979a, b) 1978 Almeida (personal communication)
4.	Red hake G.B.	1963–74 Clark and Brown (1977) 1975–78 unpublished data	1963–77 Almeida et al. (1979a) 1978 ICNAF Summ. Doc. 79/VI/30
5.	Red hake S.N.E.	1963–74 Clark and Brown (1977) 1975–77 Almeida et al. (1979b) 1978 unpublished data	1963–77 Almeida et al. (1979b) 1978 Almeida (personal communication)
6.	Red hake G.B. and S.N.E.	1963–74 calculated from Clark and Brown (1977) 1975–78 unpublished data	1963–77 calculated from Almeida et al. (1979a, b)
7.	Cod G.B. and S.N.E.	1963–74 calculated from Clark and Brown (1977) 1975–78 unpublished data	1963–77 Serchuk et al. (1979) 1978 Serchuk (personal communication)
8.	Haddock G.B.	1963–74 Clark and Brown (1977) 1975–78 unpublished data	1963–78 Clark and Overholtz (1979) 1978 Clark (personal communication)
9.	Pollock G.B., S.N.E., and G.M.	1963–74 calculated from Clark and Brown (1977) 1975–78 unpublished data	1963–77 Clark et al. (1978) 1978 Clark (personal communication)
10.	Yellowtail flounder G.B.	1963–78 McBride and Sissenwine (1979)	1963–78 McBride and Sissenwine (1979)
11.	Yellowtail flounder S.N.E.	1963–78 McBride and Sissenwine (1979)	1963–78 McBride and Sissenwine (1979)
12.	Winter flounder G.B.	1963–74 Clark and Brown (1977) 1975–78 unpublished data	1963–76 ICNAF Stat. Bull. Vol. 13–26 1977–78 ICNAF Summ. Doc. 78/VI/28 and 79/VI/30 5Z catches prior to 1968 prorated
13.	Winter flounder S.N.E.	1963–74 Clark and Brown (1977) 1975–78 unpublished data	1963–76 ICNAF Stat. Bull. Vol. 13–26 1977–78 ICNAF Summ. Doc. 78/VI/28 and 79/VI/30
14.	Summer flounder S.N.E.	1963–78 unpublished data	1963–76 ICNAF Stat. Bull. Vol. 13–26 1977–78 ICNAF Summ. Doc. 78/VI/28 and 79/VI/30

TABLE 1. *(Continued)*

Population unit	Survey population measure	Catch
15. Total flounder G.B. and S.N.E.	1963–78 unpublished data	1963–76 ICNAF Stat. Bull Vol. 13–26 1977–78 ICNAF Summ. Doc. 78/VI/28 and 79/VI/30
16. Butterfish G.B. and S.N.E.	1963–74 Clark and Brown (1977) 1975–78 unpublished data	1963–76 ICNAF Stat. Bull. Vol. 13–26 1977–78 ICNAF Summ. Doc. 78/VI/28 and 79/VI/30
17. River herring G.B. and S.N.E.	1963–78 unpublished data	1963–76 ICNAF Stat. Bull. Vol. 13–26 1977–78 ICNAF Summ. Doc. 78/VI/28 and 79/VI/30
18. Shortfinned squid G.B. and S.N.E.	1963–74 calculated from Clark and Brown (1977) 1975–78 unpublished data	1963–69 Lange (personal communication) 1970–76 ICNAF Working Pap. 78/II/2 1977–78 Lange (personal communication)
19. Longfinned squid G.B. and S.N.E.	1963–74 calculated from Clark and Brown (1977) 1975–78 unpublished data	1963–69 Lange (personal communication) 1970–76 ICNAF Working Pap. 78/II/2 1977–78 Lange (personal communication)
20. Total squid G.B. and S.N.E.	1963–74 calculated from Clark and Brown (1977) 1975–78 unpublished data	1963–69 Lange (personal communication) 1970–76 ICNAF Working Pap. 78/II/2 1977–78 Lange (personal communication)
21. Dogfish G.B. and S.N.E.	1963–78 unpublished data	1963–76 ICNAF Stat. Bull. Vol. 13–26 1977–78 ICNAF Summ. Doc. 78/VI/29 and 79/VI/30
22. Bluefish G.B. and S.N.E.	1963–78 unpublished data	1963–76 ICNAF Stat. Bull. Vol. 13–26 1977–78 ICNAF Summ. Doc. 78/VI/28 and 79/VI/30
23. Scup G.B. and S.N.E.	1963–74 calculated from Clark and Brown (1977) 1975–78 unpublished data	1963–78 ICNAF Stat. Bull. Vol. 13–26 1977–78 ICNAF Summ. Doc. 78/VI/28 and 79/VI/30
24. Total finfish and squid G.B. and S.N.E.	1963–74 calculated from Clark and Brown (1977) 1975–78 unpublished data	1963–76 ICNAF Stat. Bull. Vol. 13–26 1977–78 ICNAF Summ. Doc. 78/VI/28 and 79/VI/30

Population unit	VPA Population measure	Catch
25. Herring G.B. and S.N.E.	1964–79 Sissenwine (personal communication)	1963–77 Anthony and Waring (1981) 1978 ICNAF Summ. Doc. 79/VI/30
26. Mackerel NW Atl.	1964–79 Anderson and Overholtz (1979)	1963–78 Anderson and Overholtz (1979)
27. Silver hake	1964–79 Almeida (personal communication)	1963–77 Almeida and Anderson (1979a) 1978 ICNAF Summ. Doc. 79/VI/30

TABLE 1. (*Concluded*)

	Population unit	VPA population measure	Catch
28.	Cod G.B. and S.N.E.	1964–79 Serchuk (personal communication)	1963–77 Serchuk et al. (1979) 1978 Serchuk (personal communication)
29.	Haddock G.B.	1964–78 Clark and Overholtz (1979) 1979 Clark (personal communication)	1963–77 Clark and Overholtz 1978 Clark (personal communication)

[a]The address of all persons cited by personal communication is Northeast Fisheries Center, Woods Hole Laboratory, Woods Hole, MA 02543, USA.

(G.B. + S.N.E.), between mackerel (VPA, Northwest Atlantic) and silver hake (VPA, G.B.), between red hake (S.N.E.) and cod (G.B. and S.N.E.), and between silver hake (VPA, G.B.) and dogfish (G.B. + S.N.E.) could reflect actual interactions, although in some cases, positive interaction coefficients seem more likely. Because only 4% of the values of PCC given in Table 2 are significant at the 5% level, it is likely that many, if not all, of these significant values are the result of type I errors. There is even a stronger central tendency (toward PCC = 0) than would be expected if there were no interactions (Fig. 3). Therefore, it is not valid to interpret significant values of PCC in Table 2 as reliable evidence of population interactions. Perhaps a higher proportion of significant PCCs would occur if the model was only applied to situations where interactions were expected. Unfortunately, expectations of an interaction are often based on informal scanning of the data (thus the analysis may be prone to type I errors). It is possible to hypothesize interactions prior to analysis based on feeding habits studies, but important interactions probably occur during larval stages where little biological data are available.

It is interesting that significant values of PCC are more frequent when VPA population measures are used as a dependent variable than when survey measures are used. In fact, 10% of the models fitted to VPA data indicate significant population interactions. Perhaps this implies that VPA results are a better measure of population size then the survey results. Silver hake and cod VPAs are not highly correlated with survey catch per tow data. On the other hand, haddock VPA and survey results are correlated, and PCCs for interactions based on these two haddock population measures are in general agreement.

Although there are more significant PCCs for VPA population measures than would be expected as a result of type I errors alone, it is still dangerous to interpret any specific significant value of PCC as meaningful as some type I errors probably occur.

The results of regressions with a population measure (independent variable) lagged also provides little evidence of interactions (Table 3). Of the 198 regressions, 9 values of PCC were significant at the 5% level and 2 at the 1% level, almost exactly as would be expected due to type I errors. Estimates of interaction coefficients (c_{ij}) were negative for 135 of 198 regressions and 8 of 9 regressions where the parameter estimate was statistically significant at the 5 or 1% levels. This supports the assumption that lagged population measures represent predators.

To examine the sensitivity of the results of Tables 2 and 3 to the fitting method, the nonlinear fitting procedure discussed in the previous section was applied to yellowtail flounder (Georges Bank) with haddock (Georges Bank survey data) as a potential interacting population (independent variable) and to longfinned squid (Georges Bank and Southern New England combined) with winter flounder (Georges Bank) as a potential interacting population (in dependent variables). These population combinations were examined because they represent a case of low PCC (0.0 for yellowtail flounder–haddock) and of high PCC (−0.60 for longfinned squid–winter flounder).

Because the nonlinear fitting procedure may converge to different sets of parameter estimates (different local minimum) depending on initial parameter values, several attempts were made to fit equation (8) for each of the combinations of population units. The resulting sets of parameter estimates and error sums of squares are given in Table 4. Note that for all three fitting attempts for yellowtail flounder–haddock and for both fitting attempts for longfinned squid–winter flounder, about the same error sums of squares are obtained. Yet for the yellowtail flounder–haddock example, parameter estimates vary sharply between fitting attempts. The parameter estimates are more consistent between fitting attempts for longfinned squid–winter flounder where some of the estimates are significant at the 5% level and are similar to those obtained by the linear fitting method where estimates of a and c were 1.55 and −0.54, respectively. The partial correlation coefficient of the interaction term based on the nonlinear fitting method is −0.64 which is similar to the value of −0.60 obtained from the linear fitting method. Thus, application of the nonlinear fitting method essentially confirms results obtained by the linear method.

There are four possible explanations why the approach considered in this paper failed to provide empirical evidence of population interactions: (1) the data base does not adequately describe population size; (2) the data available are not representative of a suitable experimental design for estimating parameters as a result of colinearity of variables; (3) productivity of particular fish populations considered is not significantly dependent on the abundance of other fish populations; and (4) the models considered are inadequate for describing fish population dynamics.

There is some evidence that the failure to demonstrate empirically species interactions reflects the quality of available data. Survey results are subject to significant sampling variation, and occasionally particular observations of abundance may be anomalous because of unknown factors. Statistically significant interaction coefficients occur more frequently when VPA results are used as a measure of population size rather than survey population measures. This may

TABLE 2. Partial correlation coefficients (×100) for the interactions between combinations of 29 measures of population size based on the linearized version of equation (2). The model was used to describe the dynamics of the population measures listed vertically. The horizontally listed population measures were considered as independent variables. An * below any coefficient indicates statistical significance at the 5% level.

Populations (dependent variables)	Populations (independent variables)																												
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1. Silver hake G.B.	—			26		18	22	−29	−03	−29		−19			−22	16	−05	22	16	23	−13	18	47	−15	21	−14		−14	−26
2. Silver hake S.N.E.		—			−27	03	−11		−41		−19		04	28	−30	−14	02	−19	−35	−30	−18	22	32	−21	−07	−23			
3. Silver hake G.B. and S.N.E.			—	21	−09	15	05	−03	−26	−21	−11	−05	06	11	−18	−05	−40	−02	−20	−13	−13	13	36	18	−20	−15		−06	−03
4. Red hake G.B.	−46		−38	—			03	−41	−15	−37		−21			−34	14	−24	04	32	21	−40	39	45	−46	−37	−09	−40	−40	−43
5. Red hake S.N.E.		05	−29		—		−53*		−43		25		02	−09	00	−27	19	−48	−06	−38	−13	00	−01	−34	19	22			
6. Red hake G.B. and S.N.E.	−58*	00	−27			—	−32	−21	−20	−11	00	−36	−09	07	−09	00	00	−17	05	−10	−21	14	25	−35	−09	14	−26	−16	−20
7. Cod G.B. and S.N.E.	−18	−02	−12	−06	03	−02	—	−18	−01	−26	04	04	09	−17	06	−03	−01	05	−04	00	−18	07	19	−06	−10	06	−28		−17
8. Haddock G.B.	18		08	17		52*	−27	—	13	09		−17			11	−20	−04	10	10	03	40	−34	31	36	34	09	03	09	
9. Pollock G.M., G.B., and S.N.E.	19	04	08	21	02	14	−10	−20	—	−17	−18	−41	−28	−11	−25	−05	−10	12	11	12	−36	03	13	−34	−08	11	−12	−15	−16
10. Yellowtail flounder G.B.	22		15	07		08	09	00	38	—		−04			31	15	00	33	−17	13	−18	−20	−14	−05	−01	16	01	07	03
11. Yellowtail flounder S.N.E.		11	20		01	12	−19		21		—		−15	−19	−10	08	03	25	−10	09	13	−29	04	09	06	04		14	
12. Winter flounder G.B.	33		17	22		37	07	07	35	02		—			05	21	−11	21	31	33	34	−06	33	35	−04	−15	03	05	07
13. Winter flounder S.N.E.		−09	02		22	29	−36		30		07		—	27	−05	33	−39	11	14	16	26	03	28	20	−16	09		09	
14. Summer flounder S.N.E.		−27	−21		−09	−14	30		05		11		−28	—	18	−08	−22	−02	20	11	−24	31	−11	−23	−08	27		−25	−25
15. Total flounder G.B. and S.N.E.	27	08	20	20	22	21	−41	02	51*	−40	−04	29	00	−22	—	25	00	48	18	19	03	26	04	01	07	01	−16	10	05
16. Butterfish G.B. and S.N.E.	26	00	12	26	−01	14	08	−02	06	07	−01	−02	−24	04	00	—	−13	09	14	−06	24	03	00	18	06	10	19	−04	01
17. River herring G.B. and S.N.E.	42	21	36	40	24	43	−03	47	58*	−05	06	36	27	18	08	34	—	40	−37	13	20	−26	34	41	−01	−32	26	46	47
18. Shortfinned squid G.B. and S.N.E.	15	−03	01	31	14	28	13	−04	−23	−24	−01	03	10	01	−05	−31	−11	—	11	14	08	02	46	−06	−13	−10	01	−06	−04
19. Longfinned squid G.B. and S.N.E.	−34	50*	08	−32	−01	−27	03	−21	−29	17	13	−60*	−13	−24	10	−16	64*	−18	—	−19	45	−07	−26	−41	−38	−27	−21	−04	−21
20. Total squid G.B. and S.N.E.	−11	43	24	−07	05	−02	16	−08	−18	01	01	−53*	−14	−20	−06	−07	51*	05	−01	—	−32	−14	06	−22	−41	−08	−17	−10	−04
21. Dogfish G.B. and S.N.E.	31	09	24	37	28	44	30	04	13	13	00	−43	−06	18	04	16	−10	12	09	12	—	19	37	26	00	−23	20	14	10
22. Bluefish G.B. and S.N.E.	13	−02	07	00	21	11	−13	−08	06	20	07	−06	−08	09	18	06	−25	−06	13	03	−24	—	−31	−16	−11	16	11	−12	−09
23. Scup G.B. and S.N.E.	−06	00	−02	22	02	11	−12	−12	−13	−01	02	−37	−10	10	09	00	−15	−16	−06	16	34	25	—	−28	−05	00	09	−08	−09
24. Total finfish and squid G.B. and S.N.E.	42	02	21	54*	44	60*	13	−18	27	−07	01	57*	−22	20	01	31	−33	18	23	30	−14	27	59*	—	−25	−14	15	−10	−10
25. Herring VPA G.B. and S.N.E.	−11	41	26	18	32	31	−16	12	−12	04	31	−41	31	−02	22	−01	05	36	34	45	30	26	25	−21	—	−13	21	12	13
26. Mackerel VPA NW Atl.	−19	−17	−29	−31	−50*	−54*	−05	−30	−05	−53*	−29	31	−20	−28	−30	−30	38	15	−26	−03	−21	−18	−28	−32	19	—	50*	00	−23
27. Silver hake VPA G.B.				05		14	11	−60*	−06	−22		02			18	−08	−55*	−05	−07	−09	−58*	27	−06	−64*	−49	−28	—	−59*	−62*
28. Cod VPA G.B. and S.N.E.	08	09	10	46	−30	17		−34	−12	−43	−41	−36	−38	−28	−50*	−06	−06	−15	−07	−11	−31	−29	−62*	−38	−14	−38	−21	—	−16
29. Haddock VPA G.B.	25		34	15		44	07		−15	−08		−17			−15	−47	−01	−17	−12	−22	−02	−27	−14	−03	−35	−03	−18	−02	—

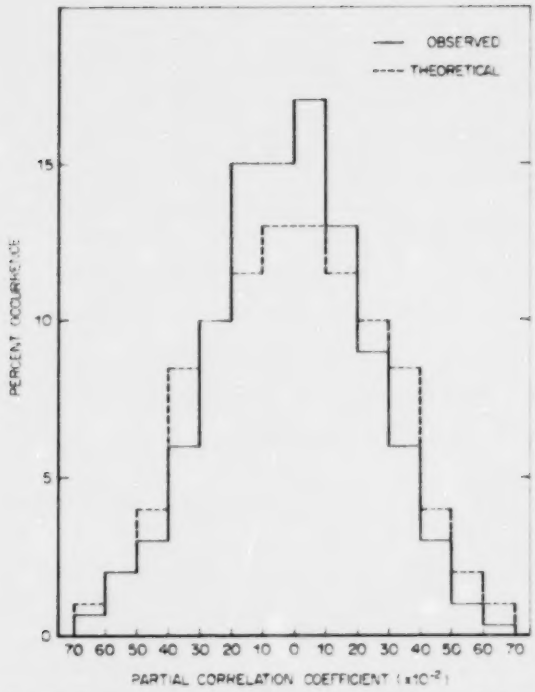

FIG. 3. Histogram of calculated partial correlation coefficients (PCC) and theoretical distribution of sample estimates of PCC when drawn from a population with true PCC = 0.

indicate that interactions are obscured by shortcomings of survey data. Nevertheless, the data base describing population abundance and catch for the area off the northeastern USA is comparable or better than such data bases for other regions of the world.

Even if the data base was vastly improved, it may not be possible to demonstrate population interactions given the natural time sequence of events in the fishery. To attribute components of variability to specific factors, it is desirable to collect data describing the response variable (dependent variable) based on an experimental design where each factor is varied orthogonally. Of course, none of the variables considered in these analyses have been controlled in the past. Therefore, some colinearity between variables occurs, and this may obscure the significance of particular factors (such as interactions between species).

Obviously, the models considered here (equations (2) and (8)) are simplistic representations of population dynamics. There are numerous characteristics of population dynamics that are ignored in these models. Of particular importance is their failure to treat the recruitment process explicitly. Fish production is not a smooth function of population size as is implied by simple logistic type models. The models assume a constant carrying capacity and that populations will recover to this level logarithmically. Hennemuth et al. (1980) indicate that the log normal probability density function is suitable for describing the distribution of year-class sizes. The infrequent occurrence of strong year-classes profoundly affects population abundance, yet such rare events are not compatible with the simple models considered here. The effect of predation of young fish on recruitment is not adequately modeled by simply incorporating a time lag.

More complex models involving combinations of more than two species were not considered. Such models would have few degrees of freedom, and our biological understanding is inadequate to determine the proper combinations in advance of parameter estimation. The shotgun approach used for pairs of populations is only practical for combinations of two populations.

The occurrence of strong year-classes (as defined in the previous section) on Georges Bank (Table 5) is summarized as follows: cod, haddock, silver hake, and yellowtail flounder during 1958; cod, haddock, and silver hake during 1959; silver hake and herring during 1960; mackerel, herring, yellowtail flounder, and silver hake during 1961; haddock and silver hake during 1962; haddock during 1963; cod and herring during 1964; yellowtail flounder during 1965; mackerel, haddock, and herring during 1966; red hake and mackerel during 1967; red hake, yellowtail flounder, and mackerel during 1968; red hake, haddock, and mackerel during 1969; herring during 1970; cod during 1971; haddock during 1972; longfinned squid during 1973; silver hake and mackerel during 1974; cod, haddock, red hake, yellowtail flounder, longfinned squid, and shortfinned squid during 1975; herring, sand lance, and shortfinned squid during 1976; mackerel, sand lance, shortfinned squid, and yellowtail flounder during 1977; and mackerel, sand lance, and shortfinned squid during 1978. There is no obvious relationship among these species.

The co-occurrence of strong year-classes may indicate either the occurrence of environmental conditions that are mutually favorable to two or more populations, or some form of biological symbiosis. The former interpretation seems more likely. The lack of co-occurrence of strong year-classes of two species may indicate either competition or predation.

There are nine combinations of populations for which co-occurrence of strong year-classes does not occur (Table 6). Silver hake, sand lance, and/or longfinned squid are included in each of these combinations. Silver hake (involved in five of the nine combinations) is an important fish predator. Sand lance (involved in three of the nine combinations) is an important fish prey item. Longfinned squid (involved in three of the nine combinations) may be important as both a predator and prey species. Thus, the lack of co-occurrence of strong year-classes does provide some qualitative evidence of biologically reasonable population interactions. Of course, when predator–prey interactions are considered, it may be more meaningful to consider the relationship between the occurrence of strong year-classes of prey species and the overall abundance of predators.

It has been hypothesized that for the North Sea, the decrease in large predators (predominantly cod) resulted in an increase in abundance of smaller species such as Norway pout. In the Georges Bank area, smaller species such as sand lance, shortfinned squid, and longfinned squid have become more abundant in recent years and strong year-classes of some or all of these species have not coincided with strong predator year-classes (cod and silver hake). Nevertheless, predatory

TABLE 3. Partial correlation coefficient (×100) for the interactions between 29 measures of population size and 8 lagged measures assumed to represent predators. An * or ** below any coefficient indicates statistical significance at the 5 or 1% level, respectively.

	Populations (dependent variables)	Populations (independent variables, lagged by 1 yr)							
		1	2	3	7	21	22	27	28
1.	Silver hake G.B.	—			−22	−16	20		−02
2.	Silver hake S.N.E.		—		03	08	32		−07
3.	Silver hake G.B. and S.N.E.		−50	—	−21	00	27		−18
4.	Red hake G.B.	−20		−24	−01	−16	21	01	−17
5.	Red hake S.N.E.		−11	−19	−28	−07	−06		05
6.	Red hake G.B. and S.N.E.	−20	−26	−26	−24	−11	−06	−01	−05
7.	Cod G.B. and S.N.E.	03	21	17	—	−19	−16	04	
8.	Haddock G.B.	−62 *		−37	−58 *	−22	16	−01	−15
9.	Pollock G.M., G.B., and S.N.E.	−60 *	−24	−45	−17	−28	31	−19	−21
10.	Yellowtail flounder G.B.	09		−07	−22	−23	−36	−34	−08
11.	Yellowtail flounder S.N.E.		−07	−10	−42	01	−22		−11
12.	Winter flounder G.B.	−10		−01	−14	−12	23	04	−04
13.	Winter flounder S.N.E.		−20	−03	−21	02	−11		−05
14.	Summer flounder S.N.E.		−02	−12	16	−71 **	23		−36
15.	Total flounder G.B. and S.N.E.	01	−20	−18	−65 *	12	−20	−21	01
16.	Butterfish G.B. and S.N.E.	−14	−36	−34	02	−19	12	−23	−24
17.	River herring G.B. and S.N.E.	46	−18	20	−23	11	04	16	07
18.	Shortfinned squid G.B. and S.N.E.	−24	−39	−41	−38	−09	39	01	−23
19.	Longfinned squid G.B. and S.N.E.	−26	14	−07	14	−42	−07	03	15
20.	Total squid G.B. and S.N.E.	−23	−05	−18	−04	−52	25	09	06
21.	Dogfish G.B. and S.N.E.	−10	15	08	−05	—	24	−13	01
22.	Bluefish G.B. and S.N.E.	−23	00	−14	05	18	—	−32	−16
23.	Scup G.B. and S.N.E.	−18	−07	−14	01	−49	14	−24	−17
24.	Total finfish and squid G.B. and S.N.E.	−22	−10	−20	−66 *	34	−18	−21	
25.	Herring VPA G.B. and S.N.E.	−14	−15	−18	−33	−30	09	15	−15
26.	Mackerel VPA NW Atl.	−31	17	−04	−27	−02	06	21	−25
27.	Silver hake VPA G.B.				−21	−14	22	—	−62 *
28.	Cod VPA G.B. and S.N.E.	−36	−33	−55		−45	63 *	06	—
29.	Haddock VPA G.B.	−81 **		−44	−40	−16	38	14	−19

TABLE 4. Results of fitting equation (8) using nonlinear method for yellowtail flounder and haddock of Georges Bank (YT-HAD) and for longfinned squid of Georges Bank and southern New England and winter flounder of Georges Bank (LONGF SQU-W FLO). An * indicates significant difference from zero at the 5% level.

	a	b	q	c	Error SS
YT-HAD					
Case 1	0.44	0.0480	9.5×10^{-5}	−0.0004	1.68
Case 2	0.12	0.0006	5.7×10^{-5}	−0.0030	1.68
Case 3	0.01	−0.0010	3.5×10^{-5}	−0.0015	1.71
LONGF SQU-W FLO					
Case 1	1.74*	0.1255	-1.0×10^{-4}	−0.68*	2.29
Case 2	1.63*	0.196	-2.7×10^{-4}	−0.71*	2.24

fish have been abundant during the recent period of increased abundance of smaller species. Cod stocks during recent years have been more abundant than during the early 1960s (Serchuk et al. 1979). Silver hake are somewhat less abundant but dogfish and bluefish (year-class strength data not available) have been relatively abundant during this period as indicated by bottom trawl survey data. In general, there is no evidence of an overall decrease in fish predators that would account for the apparent increase in smaller fish species.

Dietary similarity between mackerel and herring indicates the possibility of competition between these species (Maurer 1976). However, the data on year-class strength indicate that herring and mackerel both had strong year-classes in 1961 and again in 1966. Although extremely strong year-classes of herring and mackerel have not occurred (1960 for herring and 1967 for mackerel), available data do not support the existence of population interactions.

Although the occurrence of statistically significant interaction coefficients based on equation (2) could be attributed to chance, it is instructive to examine whether they could be logically related to the occurrence of strong year-classes. The significant interactions between stocks that occupy Georges Bank for which strong year-classes were identified were mackerel and yellowtail flounder (PCC = −0.53), silver hake and mackerel (PCC = −0.64), silver hake and haddock (PCC = −0.60), and silver hake and cod (PCC = −0.59). There is no obvious interrelationship between the occurrence of mackerel and yellowtail flounder strong year-classes, but for mackerel and silver hake it appears that strong silver hake year-classes preceded strong mackerel year-classes in the mid-1960s. Thus, peak abundance of silver hake and mackerel did not coincide. However, in the 1970s there is evidence of relatively good year-classes for both species in 1975. It is unclear whether high abundance of silver hake during the mid-1960s depressed mackerel production or whether the significant fit of the interaction term of equation (2) resulted from the chance timing of strong year-classes.

There is no apparent explanation for the silver hake and haddock negative interaction coefficient based on consideration of the occurrence of strong year-classes. The cod strong

TABLE 5. Occurrence of "strong" year-classes on Georges Bank. (*, Strong year-class (top 25% of year-classes and/or peak relative to adjacent years); —, other year-classes; NA, no data available.)

	Stock									
Year	Cod	Haddock	Silver hake	Red hake	Yellowtail flounder	Mackerel	Herring	Sand lance	Shortfinned squid	Longfinned squid
1954	NA	*	—	NA	NA	NA	NA	NA	NA	NA
1955	NA	—	—	NA	NA	NA	NA	NA	NA	NA
1956	NA	—	—	NA	—	NA	NA	NA	NA	NA
1957	NA	—	—	NA	—	NA	NA	NA	NA	NA
1958	—	*	*	NA	*	NA	NA	NA	NA	NA
1959	*	*	*	NA	—	NA	NA	NA	NA	NA
1960	—	—	*	NA	—	—	*	NA	NA	NA
1961	—	—	*	NA	—	*	*	—	NA	NA
1962	—	*	*	NA	*	—	—	—	NA	NA
1963	—	*	—	NA	—	—	—	—	—	—
1964	*	—	—	NA	—	—	*	—	—	—
1965	—	—	—	NA	*	—	—	—	—	—
1966	*	**[a]**	—	NA	—	*	*	—	—	—
1967	—	—	—	*	—	*	—	—	—	—
1968	—	—	—	*	*	*	—	—	—	—
1969	—	**[a]**	—	*	—	*	—	—	—	—
1970	—	—	—	—	—	—	*	—	—	—
1971	*	—	—	—	—	—	—	—	—	—
1972	—	**[a]**	—	—	—	—	—	—	—	—
1973	—	—	—	—	—	—	—	—	—	*
1974	—	—	*	—	—	*	—	—	—	—
1975	*	*	—	*	**[a]**	—	—	—	*	*
1976	—	—	—	—	—	—	*	*	*	—
1977	—	—	—	—	*	—	NA	*	*	—
1978	—	*	—	—	NA	*	NA	*	*	—

[a]These year-classes were larger than adjacent years, but all year-classes in the period 1965–74 for haddock and 1970–76 for yellowtail flounder (1977 is still unknown) were relatively small.

TABLE 6. Co-occurrence of strong year-classes on Georges Bank. +, Co-occurrence in one or more years; −, no years of co-occurrence.

		1	2	3	4	5	6	7	8	9	10
1	Cod		+	+	+	+	+	+	−	+	+
2	Haddock	+		+	+	+	+	+	−	+	+
3	Silver hake	+	+		−	−	+	+	−	−	−
4	Red hake	+	+	−		+	+	+	+	+	+
5	Yellowtail flounder	+	+	−	+		+	+	+	+	+
6	Mackerel	+	+	+	+	+		+	+	+	+
7	Herring	+	+	+	+	+	+		+	+	−
8	Sand lance	−	−	−	+	+	+	+		+	−
9	Shortfinned squid	+	+	−	+	+	+	+	+		+
10	Longfinned squid	+	+	−	+	+	+	−	−	+	

year-classes of 1964 and 1966 recruited while the silver hake population was declining (the latter's strong year-classes of 1958–62 were being depleted by natural mortality and heavy fishing). Again, the negative interaction coefficient may only reflect the chance timing of strong year-classes. This situation demonstrates the difficulty associated with analysis of data that are not the result of planned experimental manipulation of independent variables, but are instead confounded by temporal factors.

Conclusions

There is little quantitative evidence of species interactions for populations of the Georges Bank–southern New England region. This conclusion is based on analyses of substantial sets of data describing trends in the size of 29 population units. The qualitative examination of the co-occurrence (or lack thereof) of strong year-classes may indicate some interaction between the predator and prey populations. Nevertheless, the recent increase in abundance of smaller species (likely prey species) is not clearly related to a decrease in predator abundance as has been hypothesized for the North Sea.

This discussion is not intended to deny the existence of population interactions (although this is one possible explanation for the results). It is intended to indicate the difficulty associated with empirically demonstrating population interactions. Although simple heuristic models may be useful for less complex systems than the one discussed here or where population interactions are extremely strong (and therefore unambiguous), they are probably not suitable, in general, as a basis for multispecies fisheries management. A better understanding of the biological processes that determine the nature of interactions is necessary so that general principles of multispecies management may evolve.

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Energy Budget of Georges Bank[1]

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COHEN, E. B., M. D. GROSSLEIN, M. P. SISSENWINE, F. STEIMLE, AND W. R. WRIGHT. 1982. Energy budget of Georges Bank, p. 95–107. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

An energy budget of Georges Bank is described based on original data and a review of the published literature. Primary productivity of Georges Bank is extremely high (450 g C·m^{-2}·yr^{-1} or 2.97×10^{7} J·m^{-2}·yr^{-1}), apparently reflecting the rapid regeneration of nutrients on the bank unimpeded by a thermocline and the advection of nutrients from deeper waters on both sides of the bank. Zooplankton production based on biomass and a *P/B* ratio of 7 is estimated as 1.46×10^{6} J·m^{-2}·yr^{-1} (350 kcal·m^{-2}·yr^{-1}). Macrobenthos production is estimated at 7.53×10^{5} J·m^{-2}·yr^{-1} (180 kcal·m^{-2}·yr^{-1}) based on density estimates and production to biomass ratios. Exploited finfish and squid production ranged from 7.20×10^{4} to 5.31×10^{4} J·m^{-2}·yr^{-1} (17.2–12.7 kcal·m^{-2}·yr^{-1}) between the period 1964–66 and 1973–75.

Georges Bank appears to be more productive per unit area at all trophic levels than the North Sea, which is a much larger area. The difference in productivity is greater at lower trophic levels than for finfish and squid, possibly as a result of advection off Georges Bank.

Key words: energy budget, Georges Bank, food web, organic productivity

COHEN, E. B., M. D. GROSSLEIN, M. P. SISSENWINE, F. STEIMLE, AND W. R. WRIGHT. 1982. Energy budget of Georges Bank, p. 95–107. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

La description qui suit d'un budget énergétique du banc Georges est fondée sur des données originales et une analyse des travaux publiés. La productivité primaire du banc Georges est très élevée (450 g C·m^{-2}·a^{-1} ou 2.97×10^{7} J·m^{-2}·a^{-1}), reflétant, semble-t-il, un renouvellement rapide des éléments nutritifs sur le banc, qui n'est pas entravé par une thermocline, d'une part, et l'advection de ces éléments en provenance des eaux profondes de chaque côté du banc, d'autre part. La production zooplanctonique, fondée sur la biomasse et un rapport *P/B* de 7, est estimée à 1.46×10^{6} J·m^{-2}·a^{-1} (350 kcal·m^{-2}·a^{-1}). En se basant sur des estimations de densité et des rapports de production : biomasse, on estime que la production de macrobenthos est de 7.53×10^{5} J·m^{-2}·a^{-1} (180 kcal·m^{-2}·a^{-1}). La production de poissons et d'encornets exploités se situait entre 7.20×10^{4} et 5.31×10^{4} J·m^{-2}·a^{-1} (17,2 à 12,7 kcal·m^{-2}·a^{-1}) entre la période 1964–66 et 1973–75.

Le banc Georges semble plus productif, par unité de surface et à tous les niveaux trophiques, que la mer du Nord, qui a une superficie beaucoup plus étendue. La différence de productivité est plus marquée aux niveaux trophiques inférieurs qu'entre les poissons et l'encornet, possiblement par suite de l'advection hors du banc Georges.

Introduction

Georges Bank has long been a major fishing ground of North American fishermen and during the 1960s and early 1970s was the site of an intensive multispecies distant water fishery. Landings peaked in 1972 at 625 000 t, probably in excess of long-term sustainable levels. A gross static energy budget of Georges Bank was constructed to provide an estimate of total production potential and to clarify interrelationships among trophic levels. The energy budget is only one phase of the Northeast Fisheries Center's (NEFC) study of the Georges Bank ecosystem and is intended to provide a better scientific base for the exploitation and management of the multispecies fishery of the region.

The energy budget is based on results describing abundance and productivity at all trophic levels from both the published literature and original data of the Marine Resource Monitoring and Assessment Program (MARMAP) of the National Marine Fisheries Service. An energy budget may indicate inconsistencies in calculated productivity between trophic levels and identify critical pathways of energy flow. The energy budget for Georges Bank is compared with that of another major fishing area, the North Sea.

Primary Productivity

Although a great deal of phytoplankton research was con-

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ducted on Georges Bank in the first half of the century, results generally were not quantitative because phytoplankton nets were used thereby undersampling nanoplankton (Yentsch and Ryther 1959). A more quantitative description of the seasonal production cycle based on the oxygen production technique was provided by Riley (1941). His estimates of primary production are based on the light bottle–dark bottle technique. He used a surface sample and extrapolated the production of the entire water column based on the general features of the vertical production curve. His results show a maximum value in April of 0.95 g C·m^{-2}·d^{-1} followed by a decrease in May to 0.54 g C·m^{-2}·d^{-1} and a rise to 0.63 g C·m^{-2}·d^{-1} in June. There are no data for the rest of the summer; the next measurement, in September, was 0.14 g C·m^{-2}·d^{-1}.

During 1975–76 six cruises were conducted on Georges Bank and surrounding waters by United States (NEFC) and other countries of the International Commission for the Northwest Atlantic Fisheries (ICNAF). Five additional cruises were conducted cooperatively by NEFC and the USSR during 1977–78.

In 1975 and 1976 water samples were taken at 0, 10, 20, 50, 75, and 100 m for salinity, temperature, dissolved oxygen, chlorophyll, and nitrate, using PVC Niskin bottles. In addition, there were from 4 to 27 stations per cruise at which primary productivity was determined using the ^{14}C method. All analyses were carried out using standard oceanographic techniques (Strickland and Parsons 1968). Primary productivity measurements were made at 100, 50, 25, 10, and 1% light penetration depths. The appropriate light levels were obtained using neutral density filters in an on-deck simulated in situ incubator. The actual sampling depths for the different light levels were determined either by Secchi disc or by direct measurements using a Lambda submarine photometer. Incubations lasted ~4 h starting in the morning and running until afternoon (Cohen and Wright 1979). During 1977–78 the light depths were slightly different and the ^{14}C data include extracellular release of dissolved organic carbon (D.O.C.) and so are about 20% higher than the earlier samples, which did not measure D.O.C. (Thomas et al. 1978; O'Reilly and Thomas 1979; O'Reilly and Busch 1979). Therefore the 1975–76 data probably underestimate the actual production on Georges Bank.

The primary productivity data for each station during each cruise were integrated over the depth of the photic zone. The average value of g C·m^{-2}·h^{-1} for each cruise was then converted to g C·m^{-2}·d^{-1} based on the average day length during that cruise. The resulting cycle of primary productivity is shown in Fig. 1. It differs from the spring bloom pattern proposed earlier for Georges Bank (Riley 1941). Our data show an increase in the spring to a high level of productivity (about 2 g C·m^{-2}·d^{-1}) which is maintained throughout the summer and into the late fall with a decline to low winter values in November–December. There is considerable variability associated with the estimates (the standard deviation is approximately half the mean values shown) because of the relatively few observations and the patchiness of phytoplankton blooms. However, the results show a consistent seasonal pattern over the 4 yr of sampling. The differences between Riley's (1941) results and ours may be due to several possibilities. There may have been actual long-term changes in the production regime of phytoplankton on Georges Bank. However, it is more likely that the differences are due to the techniques used. Riley (1941) used the light bottle–dark bottle technique to estimate net productivity on surface samples and extrapolated to the entire water column. The more recent data used ^{14}C methods which give an estimate between net and gross production (Parsons et al. 1977).

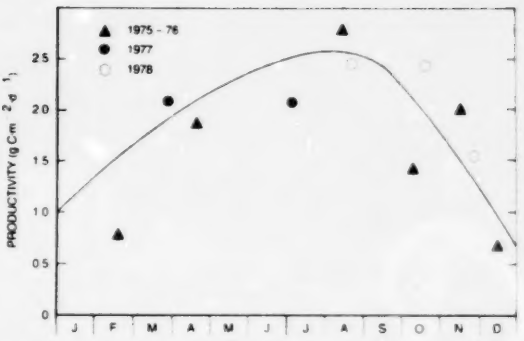

FIG. 1. Mean primary production (g C·m^{-2}·d^{-1}) versus time of year for 11 cruises on Georges Bank between late 1975 and late 1978. Each point is a mean of from 4 to 27 individual determinations. Standard deviation varied from 0.36 to 3.02 g C·m^{-2}·d^{-1}, with an average of 1.0.

Integrating our values over the year yields annual production 400–500 g C·m^{-2}·yr^{-1}, including extracellular release of D.O.C. (Cohen and Wright 1979). Analysis of NEFC chlorophyll data supports this high level of productivity (Cohen et al. 1978). This means that Georges Bank has one of the highest primary productivity levels in the ocean. Some other coastal marine estimates of annual primary productivity are (all in g C·m^{-2}·yr^{-1}): Long Island Sound, 250 (Parsons et al. 1977); Florida mangrove swamp, 600 (Odum 1971); North Sea, 90 (Steele 1974).

The high productivity of Georges Bank may be related to its unique topography and hydrography. Georges Bank is a partially closed system with respect to the surrounding waters. The mean circulation on top of Georges Bank is clockwise throughout the year (Butman et al. 1980) but there is considerable variability in the flow. Hopkins and Garfield (1981) have estimated that the residence time of water on the bank is 2 mo during the winter and 5 mo the rest of the year. Therefore a significant amount of nutrient regeneration is implied to support a high level of primary production. The shallow area on top of the bank is well mixed even during the summer, allowing nutrients regenerated in the water column and sediment to be available to the phytoplankton, unimpeded by a thermocline. Calculations based on data from 1977 (Thomas et al. 1978) show a nitrogen demand[3] range, based on the daily primary productivity, of 0.1–7 μg-at N·L^{-1}d^{-1} (mean of 2.0 μg-at N·L^{-1}·d^{-1}) in March–April and 0.5–1.65 μg-at N·L^{-1}·d^{-1} (mean of 1.0 μg-at N·L^{-1}·d^{-1}) in July. After adjusting for the different seasonal depths of the photic zone, the nitrogen demand on a m^2 basis was about

[3]The nitrogen demand was calculated using a ratio of C:N of 106:16; this is known as the Redfield ratio and it is thought to be generally applicable in the marine environment and organisms although deviations do occur (Redfield 1934).

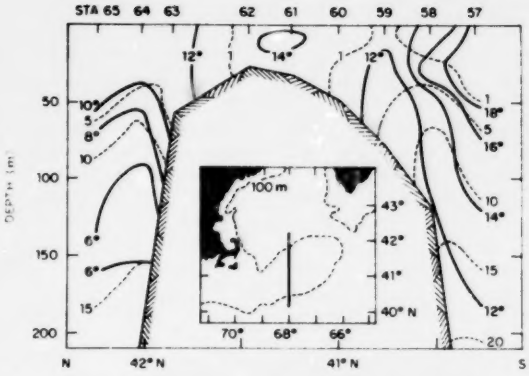

FIG. 2. Vertical section through Georges Bank at 68°W showing distribution of temperature (heavy lines, °C) and nitrate (broken lines, $\mu g \cdot at \cdot L^{-1}$) measured from R/V *Anton Dohrn* (Federal Republic of Germany) in November 1975. Vertical exaggeration about 2000:1. Heavy line on inset map shows location of section.

equal during March–April and July. At least half of the required nitrogen appears to be recycled and most of the remainder is believed to be derived from adjacent water masses. The regeneration rates of nitrogen in the water column (calculated from respiration data using an RO = 1, Thomas et al. 1978) can supply about 50% of the necessary nitrogen (range 0.13–3.96 $\mu g\text{-at } N \cdot L^{-1} \cdot d^{-1}$, mean of 0.93 $\mu g\text{-at } N \cdot L^{-1} \cdot d^{-1}$) in March–April and 70% in July (range 0.30–0.98 $\mu g\text{-at } N \cdot L^{-1} \cdot d^{-1}$, mean of 0.70 $\mu g\text{-at } N \cdot L^{-1} \cdot d^{-1}$). The benthos contributes about 7% of the total nitrogen regenerated in March–April and 3% in July (Thomas et al. 1978). The amount of nitrogen entering through rainfall has been neglected and there are no nitrogen-fixing blue-green algae on Georges Bank.

The other principal mechanism that is probably at work year-round is advection of nutrients from the deeper waters on both sides of the banks as indicated in Fig. 2. Vertical distributions of temperature and dissolved nitrate concentration along 68°W longitude (Fig. 2), from a cruise in November 1975, illustrate some persistent features of the hydrography of Georges Bank: (1) the water on the shallow top of the bank is well mixed, by both winds and tidal action; (2) there is a region of strong gradients on the south side of the bank, representing the transition to slope water conditions; (3) another frontal region exists along the northern edge of the bank, usually with weaker gradients into the waters of the Gulf of Maine; (4) nitrate, which is representative of all dissolved nutrients, is low — sometimes undetectable — on top of the bank. It increases both north and south with highest values in the deeper water. Chlorophyll distribution (not shown) is in sharp contrast with that of nutrients. The highest values of chlorophyll are found over the central portion of the bank, with very low values in the Gulf of Maine and particularly in the slope water. The nutrient-bearing water found throughout the year at depths of 150 m or more on both sides of Georges Bank is of oceanic origin. It is relatively warm but saline slope water, which flows intermittently through the Northeast Channel (sill depth 230 m) into the Gulf of Maine where it underlies the colder and fresher shelf waters (Ramp and Wright 1979). It is estimated that the amount of nitrogen that enters the Gulf of Maine through the Northeast Channel represents about 40% of the total amount needed for primary production on Georges Bank (Ramp et al. 1980). However, Ramp et al. (1980) emphasize that the flow field inside the Gulf of Maine is not yet understood and that the nutrients entering through Northeast Channel cannot all be used to support primary production on Georges Bank.

Georges Bank has a high level of primary productivity throughout the summer because of the steady supply of nutrients. The rate of primary productivity drops with decreased light levels in winter, when the critical depth (Riley 1942; Sverdrup 1953) is much shallower than the depth of the mixed layer which extends to the bottom. Phytoplankton then spend a large proportion of their time below the critical depth, and productivity is at a minimum. In spring, as the insolation increases, the critical depth deepens in relation to the mixed depth and a time is reached when photosynthesis in the water column exceeds respiration — thus the spring bloom commences. Following this, summer conditions are again reached.

Primary productivity excreted by the phytoplankton as dissolved organic carbon (D.O.C.) averages about 17% of the total primary productivity or about 77 $g\ C \cdot m^{-2} \cdot yr^{-1}$ (Thomas et al. 1978; O'Reilly and Busch 1979). This is about half of the value reported by Choi (1972) for the Scotian Shelf. The particulate organic carbon (P.O.C.) is comprised of 63% nanoplankton (235 $g\ C \cdot m^{-2} \cdot yr^{-1}$) and 37% net phytoplankton (138 $g\ C \cdot m^{-2} \cdot yr^{-1}$) (Thomas et al. 1978; O'Reilly and Busch 1979).

Platt (1971) has estimated the energy equivalents of phytoplankton. He found that at the beginning of the spring bloom, the energy equivalent was $7.68 \times 10^4\ J \cdot g\ C^{-1}$ (18.36 $kcal \cdot g\ C^{-1}$) dropping to $6.23 \times 10^4\ J \cdot g\ C^{-1}$ (14.9 $kcal \cdot g\ C^{-1}$) as the bloom passed. The mean value reported by Platt is $6.61 \times 10^4\ J \cdot g\ C^{-1}$ (15.8 $kcal \cdot g\ C^{-1}$). Expressing the yearly primary production of Georges Bank in energy equivalents gives $2.47 \times 10^7\ J \cdot m^{-2} \cdot yr^{-1}$ (5901 $kcal \cdot m^{-2} \cdot yr^{-1}$) as particulate production and D.O.C. of $5.06 \times 10^6\ J \cdot m^{-2} \cdot yr^{-1}$ (1209 $kcal \cdot m^{-2} \cdot yr^{-1}$) (as indicated in Fig. 3).

Zooplankton

Major surveys of the zooplankton of the entire Gulf of Maine–Georges Bank area were carried out by Bigelow (1926) and Fish and Johnson (1937). Since then there have been numerous investigations of zooplankton, though usually on a smaller geographic scale (Clarke 1933, 1934; Clarke and Zinn 1937; Redfield 1939; Redfield and Beale 1940, 1941; Clarke et al. 1943; Riley and Bumpus 1947; Whiteley 1948; Colton et al. 1962; Mullen 1963; Pavshtics 1963; Pavshtics and Gogoleva 1964; Sherman 1966, 1968, 1970; Sherman and Perkins 1971).

The early studies were for the most part qualitative in nature, e.g. the nets lacked flow meters. The later studies were usually of a small scale spatially and of short duration.

In 1971 NEFC began routine sampling of zooplankton with 333-μm bongos during spring and autumn bottom trawl cruises. Since 1976, plankton sampling by NEFC has been conducted on separate cruises and some smaller mesh nets.

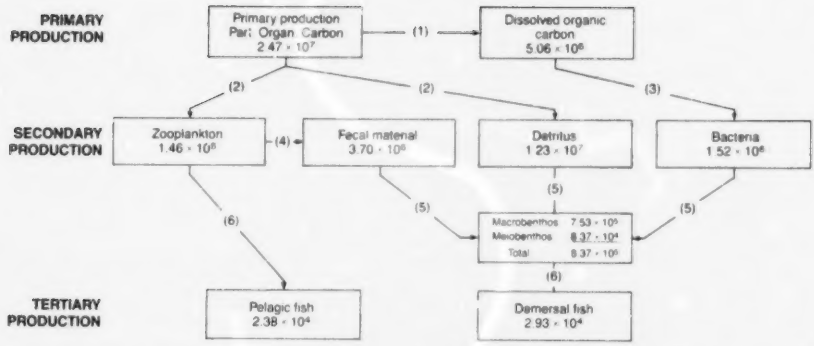

FIG. 3. Georges Bank energy budget (1973–75). All values in $J \cdot m^{-2} \cdot yr^{-1}$. Arrows indicate direction of energy flow. (1) Estimated 17% of primary production released as dissolved organic carbon (D.O.C.) (Thomas et al. 1978; O'Reilly and Busch 1979). Assumes that 1 g C = 6.6×10^4 J (15.8 kcal) (Platt 1971). Total production 2.97×10^7 $J \cdot m^{-2} \cdot yr^{-1}$. (2) Zooplankton production based on mean biomass value of 8.5 g dry $wt \cdot m^{-2}$ and *P/B* ratio as described in text. Assumes that zooplankton graze only 50% of primary production. (3) Assumption that 30% of D.O.C. is incorporated into benthic bacteria which attach to particles and enter benthos (Parsons and Seki 1971). (4) Assume assimilation efficiency of 70% (Crisp 1975). (5) Benthic production actually derived from biomass estimates and *P/B* ratios as described in text. (6) Pelagic and demersal fish production based on *P/B* ratios as described in text.

including 165- and 255-μm nets, were used in addition to 333-μm nets for zooplankton. However, data from the smaller mesh nets are not yet available. Intensive zooplankton sampling was also done from 1971 to 1978 on the ICNAF larval herring program covering the period from September to February; these data also are not yet available.

The mean density of zooplankton during 1972–75 bottom trawl surveys was 0.02 g dry $wt \cdot m^{-3}$ for both spring and fall. Assuming an average depth of 50 m, the equivalent density of zooplankton is estimated as about 1 g dry $wt \cdot m^{-2}$. Similar calculations for the 1977 and 1978 plankton surveys, which covered the period from March to November almost monthly, yielded average annual estimates of 0.037 and 0.025 g dry $wt \cdot m^{-3}$ (corresponding to 1.85 and 1.25 g dry $wt \cdot m^{-2}$) extrapolating from the early spring and late fall values to account for December through February (J. Kane, NEFC, Narragansett, RI, personal communication). These are considerably lower than the average value of 6 g dry $wt \cdot m^{-2}$ reported for the North Sea (Steele 1974). The NEFC samples are all from the 333-μm net and so even copepodite stages (1–3) of relatively small zooplankters such as *Centropages* and *Pseudocalanus*, which are very abundant on Georges Bank, were undersampled.

Riley and Bumpus (1946) report a range of values from 2.8 to 38.1 g dry $wt \cdot m^{-2}$ with a mean value of 16.7 g dry $wt \cdot m^{-2}$. However, their values probably are too high as they used a wet volume to dry weight conversion of 25%; more recent estimates have given values averaging about 10% (Kane 1979). Assuming that 2 g dry $wt \cdot m^{-2}$ is a minimum estimate of total zooplankton based on NEFC samples and that 15 g dry $wt \cdot m^{-2}$ is a maximum based on the highest values reported by Riley and Bumpus (1946) revised according to Kane's (1979) displacement volume to dry weight conversion, we estimated the range in zooplankton production as 3.10×10^5–2.31×10^6 $J \cdot m^{-2} \cdot yr^{-1}$ (74–551 $kcal \cdot m^{-2} \cdot yr^{-1}$) based on a *P/B* ratio of 7 (Crisp 1975) and a conversion factor of 2.20×10^4 $J \cdot g^{-1}$ dry wt (5.25 $kcal \cdot g^{-1}$ dry wt) (Laurence 1976). Crisp (1975) used a *P/B* ratio of 7 for *Calanus*, applied to all zooplankton; we have made the same assumption. If omnivores have a 20% growth efficiency and herbivores have a 32% growth efficiency (Steele 1974) and both have an assimilation efficiency of 70% (Crisp 1975), then between 5 and 55% of the primary production must be consumed by zooplankton. For example, conservative estimates of production and consumption, if all zooplankton are herbivores, are 3.07×10^5 $J \cdot m^{-2} \cdot yr^{-1}$ or 73.5 $kcal \cdot m^{-2} \cdot yr^{-1}$ (2 g dry $wt \cdot m^{-2} \times 2.20 \times 10^4$ J/g dry wt × 7) and 1.37×10^6 $J \cdot m^{-2} \cdot yr^{-1}$ or 328.0 $kcal \cdot m^{-2} \cdot yr^{-1}$ (3.07×10^5 $J \cdot m^{-2} \cdot yr^{-1}$/(0.32 × 0.7)), respectively. Consumption is then about 5% of primary productivity (1.37×10^6 $J \cdot m^{-2} \cdot yr^{-1}$/$2.47 \times 10^7$ $J \cdot m^{-2} \cdot yr^{-1}$). Similar calculations were done assuming all zooplankton are omnivores to obtain the upper limit. The figures agree well with the range of experimental observations made in the New York Bight and on Georges Bank by Walsh et al. (1978) and M. Dagg (Brookhaven National Lab., Upton, NY, personal communication). Based on the preceding discussion, a mean zooplankton production rate of 1.46×10^6 $J \cdot m^{-2} \cdot yr^{-1}$ (350 $kcal \cdot m^{-2} \cdot yr^{-1}$) (well within the range of available estimates) was assumed (Fig. 3).

Benthos

There has been a great deal of research on the benthic fauna of the Georges Bank–Gulf of Maine area carried out at the NEFC (Wigley 1961; Wigley and McIntyre 1964; Wigley and Emery 1968; Wigley and Theroux 1970). Most studies have been directed towards macro- and mega-benthic species although some included the meiobenthos.

The literature was reviewed to determine dominant or trophically important benthic species or taxonomic groups on Georges Bank (Wigley 1968; Bowman et al. 1976; R. L. Wigley, NEFC, personal communication). We found ~80 species that fit the above definition for one reason or another.

The literature on these or related species was examined for any data on estimated productivity; a little was found for commercially valuable species, e.g. sea scallop, but not enough to estimate total benthic productivity on Georges Bank.

An alternative method was attempted based on the use of production to biomass (P/B) ratios. The most recent estimate of benthic macrofaunal biomass on Georges Bank is 240 g wet wt·m^{-2} (R. L. Wigley personal communication). This estimated average biomass was converted into J·m^{-2} using conversions in the literature for various groups of benthic invertebrates (Brawn et al. 1968; Cummins and Wuycheck 1971; Thayer et al. 1973). The result was about 5.02×10^5 J·m^{-2}·yr^{-1} (120 kcal·m^{-2}·yr^{-1}). P/B ratios from the literature were then used to calculate the yearly productivity from the biomass data.

A variety of annual P/B estimates are available in the literature for benthic invertebrates. Values range from 0.2 for Barents Sea benthos (Zenkevitch 1956) to 5.0 for ampeliscid amphipods (Sanders 1956). The most frequently occurring P/B estimate for temperate benthic macrofauna appears to be about 1.5 (Raymont 1963; Moiseev 1969; Zenkevitch 1956). Although Sanders (1956) estimated the P/B for Long Island Sound to be between 2 and 5, considering the dominance of relatively low production molluscs and echinoderms on Georges Bank we used 1.5. This P/B ratio results in an estimate of macrobenthic productivity of 7.53×10^5 J·m^{-2}·yr^{-1} (180 kcal·m^{-2}·yr^{-1}).

A similar procedure was used to estimate meiofaunal productivity on Georges Bank. Wigley and McIntyre (1964) sampled a transect of stations south of Martha's Vineyard, ~50 nautical miles west of the southwestern border of Georges Bank. Considering only the eight stations that were less than 200 m in depth (40–179 m), the average total macrofaunal biomass was 250 g·m^{-2}, almost identical with a recent estimate for Georges Bank (240 g·m^{-2}, R. L. Wigley personal communication). Although the macrofaunal standing stocks are similar for these two areas we cannot be certain of the similarity in meiofaunal biomass or productivity; however, we have no choice but to use the available data. The meiofaunal biomass at these same eight stations ranged from 1.7 to 4.6 g·m^{-2} wet wt and averaged 2.5 g·m^{-2} (Wigley and McIntyre 1964). Using Crisp's (1975) conversion of 2 g wet wt per kcal, which is probably a minimum value for meiofauna, we get 5.23×10^3 J·m^{-2} (1.25 kcal·m^2), or a range of 3.56×10^3 to 9.62×10^3 J·m^{-2} (0.85–2.3 kcal·m^{-2}). Meiofauna biomass estimates for some other areas are as follows: Western Baltic, 1.05×10^4 J·m^{-2} (2.5 kcal·m^{-2}) (Arntz 1978); Helgoland Bay, 4.18×10^2 to 4.18×10^3 J·m^{-2} (0.1–1.0 kcal·m^{-2}) (Gerlach 1971); and the North Sea, 1.55×10^4 J·m^{-2} (3.7 kcal·m^{-2}) (McIntyre 1978). Meiofaunal biomass estimate for Georges Bank may be somewhat low. When compared on a total macro- to meiofauna biomass ratio basis, the 100:1 ratio for the Wigley and McIntyre (1964) data is greater than most other macro/meio ratios for other continental shelf areas of the temperate North Atlantic, e.g. 35:1 in Helgoland Bight (Gerlach 1971), 50:1 in Western Baltic (Arntz 1978), 40:1 in North Sea (McIntyre 1961, cited by Wigley and McIntyre 1964), and 90:1 in the English Channel (Mare 1942, cited by Wigley and McIntyre 1964). The high ratio is primarily due to one station with a high biomass of large infauna; the other seven stations had ratios ranging from 12:1 (inshore) to 120:1 (midshelf) with a mean of 40–45:1 (Wigley and McIntyre 1964). It is apparent that there is a great deal of room for error in adjusting our meiofaunal biomass; we have therefore accepted the estimate of 5.23×10^3 J·m^{-2} (1.25 kcal·m^{-2}) with the caveat that it may be low.

Using the estimate of meiofauna bimass of 5.23×10^3 J·m^{-2} (1.25 kcal·m^{-2}) we estimated annual production for Georges Bank by applying P/B ratios developed by Arntz (1978) for the Western Baltic. In the Western Baltic the estimates of the macrofaunal biomass (5.2×10^5 J·m^{-2}, 132 kcal·m^{-2}) and productivity (2.09×10^5 to 5.86×10^5 J·m^{-2}·yr^{-1}, 50–140 kcal·m^{-2}·yr^{-1}) lie between Crisp's (1975) estimate for the North Sea and our estimate for Georges Bank although as aforementioned, the meiofaunal biomass (1.05×10^4 J·m^{-2}, 2.5 kcal·m^{-2}) is twice the estimate we are using for Georges Bank. The meiofaunal P/B ratios Arntz calculated ranged between 5:1 and 12:1. These ratios, applied to our Georges Bank meiofaunal biomass estimate, yield a range of annual production of 2.62×10^4 to 6.28×10^4 J·m^{-2}·yr^{-1} (6.25 to 15 kcal·m^{-2}·yr^{-1}). This estimated range of annual meiofaunal production is less than values reported elsewhere in the North Atlantic, e.g. Steele (1974) reports 8.37×10^4 J·m^{-2}·yr^{-1} (20 kcal·m^{-2}·yr^{-1}) in the North Sea and Elmgren (1976) reports 1.09×10^5 J·m^{-2}·yr^{-1} (26 kcal·m^{-2}·yr^{-1}) in the Baltic. Considering, however, that our Georges Bank biomass estimate is minimal, the actual production is probably very similar, i.e. around 8.37×10 J·m^{-2}·yr^{-1} (20 kcal·m^{-2}·yr^{-1}). Based on these calculations the meiofauna appear to contribute only about 10% of the total benthic productivity on Georges Bank. This is much less than the reported relative contribution of the meiofauna elsewhere in the North Atlantic, e.g. Steele (1974) reports a value of 40% in the North Sea and Elmgren (1976) estimates one of 49% in the Baltic. This may reflect the fact that macrobenthos on Georges Bank can feed directly on living phytoplankton due to strong vertical mixing and shallow depths, resulting in a relatively higher proportion of macrobenthic production than found in the North Sea.

Although in general the meiofaunal benthic production may contribute less than 50% of macrofaunal production in temperate waters, the meiofauna has a much higher metabolism and rate of food consumption. Gerlach (1971) estimated the meiofaunal metabolism and food consumption to be five times the macrofaunal metabolism and food consumption in Helgoland Bay, for example.

Fish

The finfish and squid biomass, production rate, and consumption rate for Georges Bank were estimated based on research vessel bottom trawl surveys and results of virtual population analysis, production to biomass ratios (P/B), and consumption to biomass ratios (C/B), respectively. The method of calculation is summarized below; further details are given by Grosslein et al. (1980).

The annual consumption and production of exploited populations of six species on Georges Bank were estimated for the period 1963–72. During this period, population size and age composition varied widely in response to fishing pressure and

TABLE 1. Geometric mean (over all ages and years considered) of production to biomass ratio (*P/B*) and consumption to biomass ratio (*C/B*).

Species	*P/B*	*C/B*
Herring	0.29	4.6
Cod	0.60	3.3
Mackerel	0.34	4.3
Silver hake	0.69	4.9
Yellowtail flounder	0.63	4.6
Haddock	0.41	3.2
All six species combined	0.46	4.1

unexplained variability in recruitment. The species considered were the yellowtail flounder (*Limanda ferruginea*), Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), silver hake (*Merluccius bilinearis*), Atlantic mackerel (*Scomber scombrus*), and Atlantic herring (*Clupea harengus harengus*). With the exception of herring, some fishing mortality occurs at age 1. Herring less than age 2 are not caught on Georges Bank. The analysis applies to fish above the age of first exploitation. These species were selected primarily because estimates of stock size in numbers by age were available over a period of at least 10 yr. The species considered (one flounder, two demersal roundfish, one semipelagic, and two pelagic species) are a reasonable cross section of the exploited finfish community of Georges Bank.

The haddock, yellowtail flounder, and silver hake populations considered in this paper are primarily located on Georges Bank during all seasons of the year. Most of the cod and herring stocks considered here are probably located on Georges Bank during the portion of the year when they are most productive, but they do migrate off Georges Bank during winter. The mackerel population ranges from Cape Hatteras to the Gulf of St. Lawrence with migrations across Georges Bank in spring and autumn. Thus only a portion of mackerel consumption and production can be attributed to Georges Bank.

Consumption is related to production by the following energy balance equation:

$$(1) \quad \alpha C = G + S + Q$$

where C is consumption, G is growth, S is reproductive material, Q is metabolism,and α is the assimilation coefficient. C, G, S, Q are all expressed in units of energy per interval of time. Production (P) will be defined as $G + S$ in this paper. C, G, S, Q, and P were calculated for each age-group of each species on a yearly basis, using stock size estimates in numbers at age calculated by virtual population analysis (VPA). Estimates of G were based on observed growth rates of the species considered. Q is estimated as a power function of weight. The assimilation coefficient, α, was assumed equal to 0.8. S was estimated for each age and species based on a review of the literature and unpublished NEFC data on fecundity, percent maturity, and age and sex ratios. The geometric means (over all years considered) of *P/B* and *C/B* ratios for each species based on the annual virtual population estimates and equation (1) are given in Table 1.

From the *P/B* and *C/B* ratios calculated for these six species and biomass estimates calculated by Clark and Brown (1977), it is possible to make a preliminary comparison of energy flow through the finfish and squid component of the Georges Bank ecosystem between 1964–66 and 1973–75. The earlier period corresponds to the beginning of the buildup of fishing pressure on Georges Bank by other than North American fleets. The later period was after several years of intense fishing pressure when total biomass of the region had declined to its lowest level according to Clark and Brown (1979).

The mean biomass of the six species considered above (herring, mackerel, cod, haddock, silver hake, and yellowtail flounder) during each period was based on VPA. Biomass estimators by VPA during recent years are particularly sensitive to estimated terminal fishing mortality rates. Nevertheless, recent VPA biomass estimates are probably realistic as estimation of terminal fishing mortality rate or the strength of recruiting year-classes are based on data from independent research vessel surveys or the catch rate of inshore juvenile fisheries (as is the case for herring).

The biomass of redfish (*Sebastes marinus*), red hake (*Urophycis chuss*), pollock (*Pollachius virens*), flounder (other than yellowtail), shortfinned squid (*Illex illecebrosus*), longfinned squid (*Loligo pealei*), and other finfish was estimated using calculations made by Clark and Brown (1977) although the specific results used here were not actually included in their published paper. All biomass estimates are expressed per unit area of Georges Bank alone. Where biomass estimates are for areas larger than (but including) Georges Bank, they were adjusted by multiplying by the ratio of the average survey catch rate on the Bank to the average survey catch rate for the larger area. This procedure assumes identical fishing power of the standard survey trawl in all areas.

Production and consumption of pollock, other flounder, and other finfish were calculated by applying the geometric mean *P/B* and *C/B* ratios for all six species considered in Table 1 (0.46 and 4.1, respectively). *P/B* ratios of 0.25 and 1.5 were assumed for redfish and squid reflecting their very slow and very rapid growth. In the case of squid (with a 1- or 2-yr life cycle) even a *P/B* ratio of 1.5 is probably conservative. *C/B* ratios of 3.0 and 7.0 were assumed for redfish and squid, respectively. The calculated production, consumption, and biomass by species group per unit area of Georges Bank are given in Table 2. Results from the later period are included in Fig. 3.

Both consumption and average biomass declined by about 42% between 1964–66 and 1973–75, but production declined by only 26%. The smaller reduction in production reflects primarily a decline in herring which have a low *P/B* ratio and the increase in squid which are assumed to have a high *P/B* ratio.

Energy Budgets — Georges Bank versus North Sea

The Georges Bank energy budget was modeled after those of Steele (1974) and Crisp (1975) for the North Sea. The energy flow and relative productivity of the North Sea is compared with that on Georges Bank in Fig. 3 and 4, where

TABLE 2. Biomass, consumption, and production of finfish and squid on Georges Bank in millions of joules per kilometre squared.

Species group	1964–66			1973–75		
	Biomass	Consumption	Production	Biomass	Consumption	Production
Cod	7 908	22 430	4 481	3 849	12 703	2 770
Haddock	18 719	67 434	8 983	1 854	5 933	761
Redfish	96	288	25	222	707	54
Silver hake	42 058	203 288	24 393	31 012	151 955	18 297
Red hake	4 535	18 594	2 088	3 351	13 740	1 540
Pollock	1 163	4 770	536	494	2 025	226
Yellowtail flounder	2 615	12 025	1 669	2 013	9 259	1 268
Other flounder	1 305	5 351	602	1 000	4 100	460
Herring	80 588	366 188	22 564	25 945	119 349	7 523
Mackerel	5 498	22 635	1 866	11 422	49 116	3 883
Other finfish	7 046	28 886	3 243	9 456	38 769	4 351
Illex	967	6 766	1 033	7 192	50 346	10 791
Loligo	264	1 845	397	1 142	7 996	1 715
Total	172 766	803 596	71 797	98 952	465 955	53 179

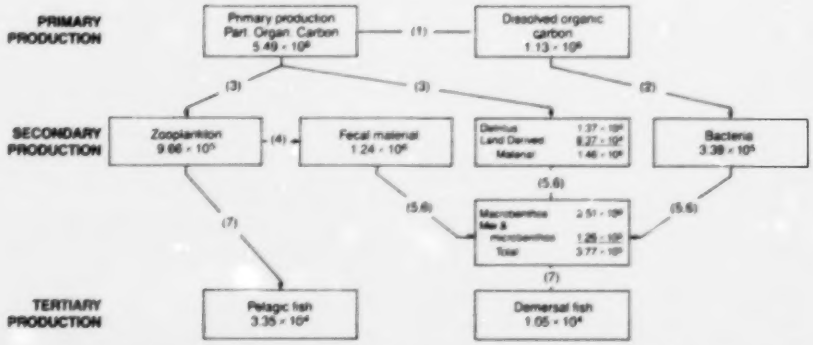

FIG. 4. North Sea energy budget (modified from Crisp 1975). All values in $J \cdot m^{-2} \cdot yr^{-1}$. Arrows indicate direction of energy flow. (1) Estimated 17% of primary production released as dissolved organic carbon (D.O.C.) (Thomas et al. 1978; O'Reilly and Busch 1979). Assumes 1 g C = 6.61 × 10^4 J (15.8 kcal) (Platt 1971). (2) Assume 30% of D.O.C. incorporated into benthic bacteria that attach to particles and enter benthos (Parsons and Seki 1971). (3) Assumption that 75% of phytoplankton is consumed by zooplankton; remainder is detritus (Crisp 1975). Zooplankton production based on biomass estimate of 6.3 g dry wt and *P/B* ratio of 7 (Crisp 1975). (4) Assume assimilation efficiency of 70% (Crisp 1975). (5) Macrobenthic production calculated from benthic biomass (8.37×10^4 J·m^{-2}·yr^{-1}) and *P/B* ratio of 3 (Crisp 1975). (6) Assumption that 13% of total energy available to benthos is left over for meio- and micro-benthos (from Crisp 1975) with further assumption of 30% ecological efficiency for meio- and micro-benthos. (7) Pelagic and demersal fish production based on catch data of 1.67×10^4 and 8.37×10^3 J·m^{-2}·yr^{-1}, respectively (Crisp 1975).

all values are shown in $J \cdot m^{-2} \cdot yr^{-1}$. Georges Bank appears to be more productive per unit area than the North Sea at all trophic levels. However, it is important to keep in mind that the North Sea is a much larger area than Georges Bank (570 000 km^2 vs. 52 579 km^2) with greater heterogeneity, containing both shallow and relatively deep areas, and with a well-developed thermocline in summer. The two areas are not strictly comparable oceanographically but do provide a useful comparison as both are temperate shelf areas, heavily exploited with similar fish species, and have what appear to be generally similar trophic structures.

PRIMARY PRODUCTION

The annual primary production in the North Sea is considered to be on the order of 100 g C·m^{-2}·yr^{-1} (Steele 1974; Crisp 1975) as compared with an estimated 400–500 g C·m^{-2}·yr^{-1} on Georges Bank. Thus it appears that Georges Bank has a level of primary production about four to five times that of the North Sea on an annual basis. Recent studies in the southern bight area of the North Sea by Mommaerts (cited in Polk 1978) indicate production as high as 220–370 g C·m^{-2}·yr^{-1}. Because this study was in a shallow (<15 m)

coastal region we have used the estimate based on earlier studies pending further investigation.

For comparison with Georges Bank we modified Crisp's energy budget for the North Sea by using the same conversion of 6.61×10^4 J·g C^{-1} (15.8 kcal·g C^{-1}) instead of 4.18×10^4 J·g C^{-1} (10 kcal·g C^{-1}) to calculate total energy produced by phytoplankton; this conversion results in a 58% increase in absolute primary production values over those used by Crisp. Thus the total primary production of the North Sea was estimated to be 6.61×10^6 J·m^{-2}·yr^{-1} (1580 kcal·m^{-2}·yr^{-1}), of which 5.49×10^6 J (1311 kcal) or 83% was available in particulate form to herbivores (Fig. 4).

Comparable figures for Georges Bank were total primary production of 2.97×10^7 J·m^{-2}·yr^{-1} (7110 kcal·m^{-2}·yr^{-1}) of which 2.47×10^7 J (5901 kcal) or 83% was assumed to be available to herbivores and omnivores (Fig. 3). The greater production on Georges Bank is probably due primarily to its shallowness. Wind and tidal mixing recycle nutrients in the water column and from the sediments on the bank as well as advecting nutrient-rich deep water from the Gulf of Maine and the slope onto the bank. However, this advection implies transport of water off the bank, and some of the production is lost in this manner.

Zooplankton Production

Crisp (1975) estimated zooplankton production in the North Sea in two ways: (1) assuming 75% of particulate phytoplankton consumed by zooplankton with a growth efficiency of 30%, and (2) a direct estimate using zooplankton biomass and assuming a *P/B* ratio of 7; these estimates were 7.53×10^5 and 7.32×10^5 J·m^{-2}·yr^{-1} (180 and 175 kcal·m^{-2}·yr^{-1}), respectively. For comparison with Georges Bank we have recalculated zooplankton production for the North Sea but with somewhat modified assumptions. We assumed that 75% of particulate carbon is consumed by zooplankton with nanoplankton consumed by microzooplankton (32% growth efficiency) which are consumed by macrozooplankton (20% growth efficiency) and net phytoplankton consumed directly by macrozooplankton (32% growth efficiency). This trophic structure is based on the work of Parsons and Lebrasseur (1979). This probably overestimated macrozooplankton production as it assumed that 100% of microzooplankton are consumed. The resulting production is only 6.53×10^5 J·m^{-2}·yr^{-1} (156 kcal·m^{-2}·yr^{-1}) even though the estimated initial amount of particulate carbon available was 58% higher than that used by Crisp (Fig. 4). Our second estimate for the North Sea was 9.66×10^5 J·m^{-2}·yr^{-1} (231 kcal·m^{-2}·yr^{-1}) derived from the same zooplankton biomass and *P/B* ratio used by Crisp (1975) but substituting the conversion of 2.20×10^4 J·g C^{-1} (5.25 kcal·g C^{-1}) for that of 1.67×10^4 J·g C^{-1} (4 kcal·g C^{-1}) used in the Crisp formulation, see Fig. 4. The average of our two estimates (149 kcal·m^{-2}·yr^{-1}) for the North Sea is only slightly higher than Crisp's values but our estimate of the proportion of particulate carbon converted to zooplankton production is somewhat lower than Crisp's values, 15 vs. 22%.

The zooplankton production for Georges Bank is 1.46×10^6 J·m^{-2}·yr^{-1} (350 kcal·m^{-2}·yr^{-1}) which is about two times as large as zooplankton production for the North Sea. This is half the ratio observed for the primary production between the two areas (Fig. 3 and 4). Better measures of zooplankton biomass on Georges Bank will be required before we can evaluate the zooplankton production estimates further. The results of calculations on the amount of phytoplankton consumed, discussed earlier in the paper, agree well with the experimental data (Walsh et al. 1978; M. Dagg personal communication). This low value is not consistent with the value of 100% used by Steele (1974) and of 75% used by Crisp (1975). This disparity implies either a major difference between the North Sea and Georges Bank in the extent of zooplankton consumption, or that the data or assumptions for one or the other location (or both) are incorrect. Assuming that the data for both areas are correct, a great deal more energy per unit area will be available to the benthos on Georges Bank than in the North Sea, because not only is the magnitude of primary productivity greater on Georges Bank but the fraction directly available to the benthos is also greater. Of course, some of the primary and secondary production is advected off the bank.

Benthic Production

We estimate total benthic production in the North Sea as 4.18×10^5 J·m^{-2}·yr^{-1} (100 kcal·m^{-2}·yr^{-1}) as compared with 8.37×10^5 J·m^{-2}·yr^{-1} (200 kcal·m^{-2}·yr^{-1}) for Georges Bank. Our North Sea estimate is based on Crisp's (1975) estimate of macrobenthos production of 2.51×10^5 J·m^{-2}·yr^{-1} (60 kcal·m^{-2}·yr^{-1}) and Steele's (1974) conclusion that macrobenthos production is 60% of the total (ignoring microbenthos). This implies meiobenthos production of 1.67×10^5 J·m^{-2}·yr^{-1} (40 kcal·m^{-2}·yr^{-1}) or twice that reported by Steele (1974). Using the direct estimates of North Sea meiofauna biomass of 3.7 kcal·m^{-2} by McIntyre (1978) and assuming a *P/B* ratio of 8.5, the midpoint of the range reported by Arntz (1978), meiobenthos production may be estimated directly as 1.20×10^5 J·m^{-2}·yr^{-1} (31 kcal·m^{-2}·yr^{-1}). Meiobenthos production of 8.37×10^4 to 1.26×10^5 J·m^{-2}·yr^{-1} (20–30 kcal·m^{-2}·yr^{-1}) for the North Sea appears consistent with Crisp's calculations; he estimated that 1.67×10^6 J (400 kcal) was consumed by macrobenthos leaving only 2.51×10^5 J (60 kcal) or 13% of available energy for meio- and micro-benthos. A *P/C* ratio of about 0.4 or 0.5 which seems reasonable for the smaller benthic organisms would be sufficient to yield 8.37×10^4 to 1.26×10^5 J·m^{-2}·yr^{-1} (20–30 kcal·m^{-2}·yr^{-1}). A *P/C* ratio of 0.7 would be required to yield 1.67×10^5 J·m^{-2}·yr^{-1} (40 kcal·m^{-2}·yr^{-1}), the additional amount needed to provide a total benthic production of 4.18×10^5 J·m^{-2}·yr^{-1} (100 kcal·m^{-2}·yr^{-1}) using Crisp's estimate of energy available to benthos.

If the total energy actually available to the benthos in the North Sea is as much higher as indicated by our estimates in the comparison with those of Crisp (3.28×10^6 vs. 1.93×10^6 J) (783 vs. 460 kcal → see Fig. 4) then total benthic production in the North Sea could be substantially higher than 4.18×10^5 J·m^{-2}·yr^{-1} (100 kcal·m^{-2}·yr^{-1}). For example, if 1.67×10^6 J (400 kcal) are consumed by macrobenthos as estimated by Crisp then nearly half or 1.60×10^6 J (383 kcal) would be left for meio- and micro-benthos, of which much more than 15% could be converted into production. Assuming, however, that the benthic production esti-

mates reported for the North Sea are approximately correct, this would imply that our absolute estimate of energy available to the benthos is too high — perhaps because the phytoplankton energy conversion of 6.61×10^4 J·g C^{-1} (15.8 kcal·g C^{-1}) is too high.

A more significant difference between the two areas is the apparent lower level of benthic production per square metre on Georges Bank relative to total energy per square metre in the system. Total benthic production on Georges Bank is $8.37 \times 10^5/2.97 \times 10^7$ (200/7110) = 2.8% of the total energy available from phytoplankton as compared with $4.18 \times 10^5/6.61 \times 10^6$ (100/1580) = 6.3% for the North Sea, based on our calculations and shown in Fig. 3 and 4. If we assume a 4.18×10^4 J·g C^{-1} (10 kcal·g C^{-1}) conversion for phytoplankton production the comparable calculations would be $8.37 \times 10^5/1.88 \times 10^7$ (200/4500) = 4.4% and $4.18 \times 10^5/4.18 \times 10^6$ (100/1000) = 10% for Georges Bank and the North Sea, respectively. Either way the benthic production on Georges Bank appears to be low compared with the North Sea by a factor of more than 2. As noted earlier it is possible that production of the meio- and micro-benthos is underestimated for Georges Bank.

If we assume that Steele's 60:40 ratio of macro- to meio-fauna production applies to Georges Bank then total benthic production on Georges Bank would be 1.26×10^6 J·m^{-2}·yr^{-1} (300 kcal·m^{-2}·yr^{-1}), an increase of 50%. This would reduce the discrepancy to a factor of somewhat less than 2 but the total benthic production on Georges Bank would still be low relative to the North Sea. One possible explanation is advective loss of plankton production from Georges Bank. Over half the total carbon would have to be lost in this way to bring the benthic production/total production ratio into line with the North Sea, using the benthic production estimate of 8.37×10^5 J·m^{-2}·yr^{-1} (200 kcal·m^{-2}·yr^{-1}) for Georges Bank, and about one-third the total would have to be lost if we use 1.26×10^6 J·m^{-2}·yr^{-1} (300 kcal·m^{-2}·yr^{-1}). Another possible explanation might be that a greater proportion of energy on Georges Bank is tied up in large relatively slow-growing molluscs and echinoderms. On the other hand, it is also possible that filter feeders on Georges Bank consume live phytoplankton to a greater extent because of the strong vertical mixing and the shallowness of the bank.

Estimates of benthic productivity are subject to many errors and neither the Georges Bank nor the North Sea estimates adequately take into account the microfauna. More detailed studies of the benthic productivity in the two regions, and a better understanding of circulation on Georges Bank, will be required to evaluate these possibilities.

Fish Production

Crisp (1975) estimated the production of North Sea pelagic and demersal fish species as 3.3×10^4 J·m^{-2}·yr^{-1} (8.0 kcal·m^{-2}·yr^{-1}) and 1.05×10^4 J·m^{-2}·yr^{-1} (2.5 kcal·m^{-2}·yr^{-1}), respectively. These estimates are based on fishery production (by assuming exploitation rates). Georges Bank production of pelagics (herring, mackerel, and squid) was 2.59×10^4 and 2.38×10^4 J·m^{-2}·yr^{-1} (6.2 and 5.7 kcal·m^{-2}·yr^{-1}) during periods of high and low biomass, respectively. The corresponding values for demersals were 4.60×10^4 and 2.93×10^4 J·m^{-2}·yr^{-1} (11.0 and 7.0 kcal·m^{-2}·yr^{-1}). Thus, the pelagic production of the two areas is similar, but the demersal production of Georges Bank is substantially higher than the North Sea.

Both the total difference and the relative difference between demersal and pelagic components of fish production between the two regions pose questions analagous to those for the benthic production. Total fish production (per square metre) on Georges Bank was less than twice that in the North Sea although primary production appears more than four times as great on Georges Bank. The pelagic fish production estimates for Georges Bank were actually less than those for the North Sea, whereas demersal fish production on Georges Bank appeared to be three to four times that of the North Sea. It is quite possible that the *P/B* ratio used for squid was too low and this would have increased the pelagic production estimate somewhat for Georges Bank, but probably not enough to change the picture drastically. Mackerel production on Georges Bank was also probably underestimated by partitioning total production of the stock according to the size of Georges Bank relative to the total area inhabited by the stock. Another likely source of error could be unaccounted production of small pelagic species or species such as sand lance on Georges Bank. There is evidence for a dramatic increase in sand lance numbers on the continental shelf of the northeastern U.S. in the latter part of the 1970s (Grosslein et al. 1980; Sherman et al. 1981). Finally, we have not yet accounted for birds and mammals but their energy requirements are thought to be relatively small in the Georges Bank area compared with that of the pelagic fish component.

Although we probably underestimated pelagic fish production on Georges Bank, it is unlikely that the estimate was low by a factor of 2.5, which is about the level of difference needed to bring the ratio of pelagic fish/zooplankton production in line with the values for the North Sea. On the other hand, to account for the relatively low level of pelagic fish production on Georges Bank through advective losses of plankton production, we have to assume about a 68% loss.

Actually, the production estimates considered here are not strictly comparable. Crisp's (1975) estimates are based on fishery yield; therefore they represent growth and recruitment. The energy of recruits is actually a minimum estimate of growth production of prerecruits. It is not production of exploitable sized fish. Crisp's estimates do not include production of reproductive material. Another factor to consider is that in any area a decade is probably insufficient time upon which to base estimates of average or sustainable fish production because of recruitment variations.

The average recruitment to biomass ratios (*R/B*) of herring, cod, mackerel, silver hake, yellowtail flounder, and haddock, are 0.16, 0.05, 0.14, 0.10, 0.06, and 0.03, respectively (Grosslein et al. 1980). Of course, *R/B* depends on the designated age at recruitment with this ratio increasing with age. In the North Sea, where small mesh nets are typically used, the *R/B* ratios are probably not significantly larger than those calculated for Georges Bank with age at recruitment designated as age 1 or 2. Assuming that annual reproductive energy is 10% of the biomass for sexually mature fish (as was assumed by Grosslein et al. (1980) for several species) *R/B* would have to be somewhat less than 10% for recruitment energy to balance reproductive energy (as not all individuals

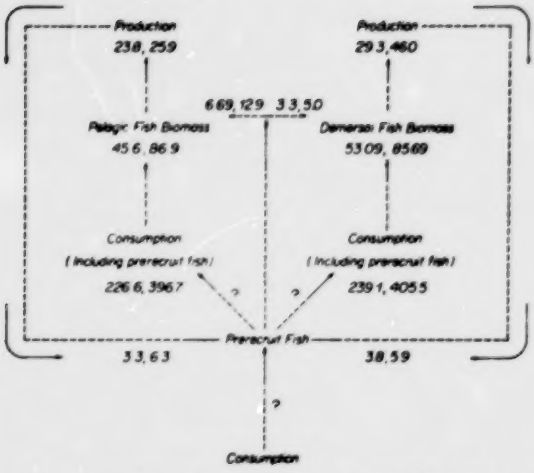

FIG. 5. Energy flow of Georges Bank finfish and squid community expressed in $J \cdot 10^3 \cdot m^{-2}$ or $J \cdot 10^3 \cdot m^{-2} \cdot yr^{-1}$. First entry of each item is for 1973–75, second entry is for 1964–66. A recruitment to biomass ratio of 0.15 and 0.06 is assumed for pelagics and demersals, respectively. Egg production is assumed to be 7% of fish biomass annually.

are mature). Thus, it is probably reasonable to compare Crisp's estimates of production with those calculated in this paper as recruitment and reproductive energy are similar in magnitude and approximately balance. The fact that recruitment and reproductive energy are similar in magnitude implies that the early life stages of fish consume much more energy than is contributed in the form of eggs. Clearly, both the production estimates reported by Crisp and those reported here underestimate the total production of the fish community (including all life stages). Further details of energy flow within the Georges Bank finfish and squid community are summarized in Fig. 5.

It is also possible to compare finfish and squid consumption in the two areas. In the North Sea, the decline in biomass of herring and mackerel during the 1960s was accompanied by an increase in biomass of certain other species, particularly the gadids. Jones and Richards (1976) indicate that the decline in herring and mackerel biomass could have released enough food energy to support the increased biomass of gadids. In the case of Georges Bank (1964–66 vs. 1973–75), the decline in herring and mackerel biomass was also accompanied by a decline in almost all demersal species including cod, silver hake, and most notably haddock. Even so, the relative change in surplus food available (assume the rate of production by fish prey is unchanged) before and after the decline in biomass of both areas is similar. The total consumption by exploitable sized fish of nine species considered by Jones and Richards for the North Sea declined by 33% between the early and late 1960s. Total exploitable sized finfish and squid consumption on Georges Bank declined by 42% between 1964–66 and 1973–75.

The consumption per square metre of Georges Bank appears higher than the North Sea: 8.03×10^5 vs. 2.3×10^5 $J \cdot m^{-2}$ (192 vs. 55 kcal $\cdot m^{-2}$) for the high biomass period and 4.64×10^5 vs. 1.51×10^5 $J \cdot m^{-2}$ (111 vs. 36 kcal $\cdot m^{-2}$) for the low biomass period. The difference in consumption between the two areas is actually smaller than these values indicate as the North Sea values only apply to nine species generally at an older age than for Georges Bank. Other finfish and squid account for 5 and 20%, respectively, of the total Georges Bank consumption during the two periods. The North Sea values typically apply to fish age 2 and older whereas the Georges Bank values apply to age 1 and older (except for herring). Nevertheless, it is likely that total consumption per unit area is higher on Georges Bank than in the North Sea, as would be expected with a higher density of fish.

In summary, the biomass and consumption of both pelagic and demersal species declined on Georges Bank (1964–66 vs. 1973–75) whereas only the former declined in the North Sea (early and late 1960s). Consumption per unit area on Georges Bank appears to be higher than in the North Sea. Although finfish and squid production per unit area is probably higher on Georges Bank than in the North Sea, the difference is surprisingly small considering the difference in productivity at other trophic levels.

Discussion

The construction of the energy budget was intended as a device to organize our data and those in the literature into a form that might make the relationship of the various trophic levels clearer. It has provided as many questions as answers and pointed out several key areas where we lack sufficient data. Our knowledge of the benthos is very incomplete. We have only a slight idea as to the production of the macrobenthos and are almost wholly ignorant of the biomass and production of the meio- and micro-fauna. Information on zooplankton production is also very limited and only recently has more complete seasonal coverage of the zooplankton been implemented.

One of the big surprises to arise out of the energy budget exercise was the very high level of primary production on Georges Bank. Previous estimates had been in the range of 200–300 g $C \cdot m^{-2} \cdot yr^{-1}$. We have revised the estimate upwards to 400–500 g $C \cdot m^{-2} \cdot yr^{-1}$ and a picture is emerging of a seasonal cycle possibly different from the classical spring-bloom cycle (Riley 1941, 1946). We now think that after an initial increase in the spring, production remains at high levels throughout the summer and into the fall. This is probably due to a combination of recycling and advection. The shallowness of Georges Bank coupled with wind and tidal mixing allows a constant supply of regenerated nutrients from the water column and benthos to reach the phytoplankton in the photic zone. Also a supply of nutrient-rich water is available from the Gulf of Maine and slope water that is advected onto Georges Bank by tidal mixing and other mechanisms. However, some of this productivity is surely lost through transport, and better understanding of the nutrient flux and circulation on Georges Bank is needed to clarify this question.

With regard to fish it is only in the production of pelagic species that there appears to be a significant discrepancy between the Georges Bank and North Sea ecosystems. More accurate accounting of the possible energy "losses" from Georges Bank may explain part of this discrepancy. However, if we examine fish production from the entire New England

shelf region from Cape Hatteras to the Gulf of Maine, including Georges Bank (corresponding to ICNAF statistical areas 5 and 6), we see that demersal fish production per unit area is about the same as for the North Sea but pelagic fish production per unit area is still lower by a factor of at least two. The total MSY of finfish and squid for the entire New England area is on the order of 1.3×10^6 tons or about 5 tons $\cdot$ km^{-2} (Hennemuth 1976). Although the MSY value overestimates actual production of recruited sized fish, in this case the value is probably conservative in comparison with the North Sea estimates of "production," which include contributions from smaller sized "prerecruits" due to the smaller mesh used in the North Sea. The MSY for the New England area is roughly equivalent to a production of 2.09×10^4 J $\cdot$ m^{-2} (5 kcal $\cdot$ m^{-2}, assuming 1 g wet weight of fish = 1 kcal = 4.18×10^3 J), of which slightly more than half, 1.09×10^4 J $\cdot$ m^{-2}, is attributed to the major pelagic species (herring, mackerel, squid, and menhaden). The comparable production for the North Sea is 4.39×10^4 J $\cdot$ m^{-2} (10.5 kcal $\cdot$ m^{-2}), of which three-quarters or 3.35×10^4 J $\cdot$ m^{-2} (8 kcal $\cdot$ m^{-2}) is attributed to pelagic fish. Thus it appears that pelagic fish production per unit area is substantially lower on the New England Shelf than in the North Sea even though the primary production levels in the Gulf of Maine and in the Middle Atlantic Bight are thought to be at least as high as 100 g C $\cdot$ m^{-2} $\cdot$ yr^{-1}. Unique hydrographic features in the New England area such as the relatively deep waters of the Gulf of Maine and the extreme seasonal temperature ranges encountered in the Middle Atlantic Bight (causing large-scale migrations in and out of the area) may reduce the productive potential somewhat. Also, losses of coastal water may occur through entrainment by Gulf Stream rings and other processes.

Mills and Fournier (1979) and Mills (1980) examined the structure and dynamics of the marine ecosystem off the coast of Nova Scotia. Primary production on the Scotian Shelf is slightly higher than in the North Sea and considerably lower than on Georges Bank. Like Georges Bank, the efficiency of energy transfer to higher trophic levels is lower for the Scotian Shelf than for the North Sea. In particular, there appears to be a deficit in pelagic fish production for both Northwest Atlantic continental shelf ecosystems when compared with the North Sea. Mills and Fournier (1979) applied a *P/B* ratio of 0.60 for pelagic fish, approximately double the ratio estimated for Georges Bank. Thus, the deficit in pelagic fish production for the Scotian Shelf might be even greater than reported by Mills and Fournier (1979).

On Georges Bank it is noteworthy that the consumption of one finfish species, silver hake, exceeds total productivity of the exploited finfish and squid community. Silver hake (like cod and squid) feed heavily on other finfish (Grosslein et al. 1980); therefore much of its consumption must be of prerecruit fish. The impact of prerecruit consumption of silver hake and other fish predators is unknown, but its potential significance is very great, particularly as its effects might be partially controlled through management.

In summary, Georges Bank seems to be more productive at all trophic levels than the North Sea, per unit area, but the paths of energy flow in each system appear to be quite different. The amount of zooplankton and benthic production is lower relative to primary production on Georges Bank than in the North Sea. Pelagic fish production on Georges Bank seems to be very much lower relative to primary production and zooplankton production compared with the North Sea. The discrepancy implies a difference in the whole food web, not just in the zooplankton portion. The ratio of demersal fish production to primary production is about the same in the two areas but again differences in the food web are apparent. Further study is needed to examine the possible export of particulate matter from Georges Bank, and in particular to elucidate the food webs in quantitative terms for comparisons with other marine ecosystems. Even after the effects of variable recruitment are accounted for, we may see some significant differences in the utilization of energy in various ecosystems.

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Interactions in Kelp Bed Ecosystems in the Northwest Atlantic: Review of a Workshop

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PRINGLE, J. D., G. J. SHARP, AND J. F. CADDY. 1982. Interactions in kelp bed ecosystems in the northwest Atlantic: review of a workshop, p. 108–115. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

Workers in eastern Nova Scotia hypothesized that (1) American lobsters (*Homarus americanus*) are the keystone predators of kelp (*Laminaria* spp.) bed ecosystems, (2) lobster populations have declined due to poor management, (3) this has permitted urchin (*Strongylocentrotus droebachiensis*) populations to explode, causing destructive grazing of macroalgae, and (4) the resultant barren system is permanent. A workshop, sponsored by fisheries management, discussed these hypotheses in light of presented papers and recommended remedial action. Participants concluded that kelp bed destruction in St. Margaret's Bay, Nova Scotia, was due to urchins but the triggering process was unclear. Allochthonous sources, kelp disease, and release from predation were discussed. Lack of historical data east and west of St. Margaret's Bay and evidence that south and west coasts of Newfoundland have not had *Laminaria* beds for possibly centuries made it difficult to assess the extent of the urchin problem along Atlantic Nova Scotia and the Bay of Fundy. Evidence was presented suggesting the urchin population increases of coastal, southern California were due to the overharvesting of at least three commercial carnivores (spiny lobster (*Panulirus interruptus*), California sheephead (*Pimelometopon pulchrum*), and the sea otter (*Enhydra lutris*)) and one herbivore (abalone (*Haliotus rufescens*)). Many natural predators of urchins were cited for the northwest Atlantic; some have suffered reduced population densities as they are of commercial importance (lobsters, cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), flounder (*Pseudopleuronectes americanus*), wolffish (*Anarhichas lupus*), etc.) whereas certain of the remainder (crabs, ducks, etc.) have had population decreases due to other activities of man. The trophic pyramid appears to have been simplified with the possible consequence that significant annual changes in carnivore densities permit the system to oscillate wildly. It was felt premature to claim the kelp bed ecosystem of St. Margaret's Bay had been permanently lost; however, it was recommended that a multispecies ecosystem approach be employed in fisheries resource management.

Key words: lobster, kelp, *Laminaria*, resource management, sea urchins, grazing, fisheries, coralline, workshop, groundfish

PRINGLE, J. D., G. J. SHARP, AND J. F. CADDY. 1982. Interactions in kelp bed ecosystems in the northwest Atlantic: review of a workshop, p. 108–115. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

Les chercheurs travaillant dans l'est de la Nouvelle-Écosse avancèrent les hypothèses suivantes : (1) les homards (*Homarus americanus*) sont les principaux prédateurs des écosystèmes de lits de laminaires (*Laminaria* spp.); (2) une mauvaise gestion est la cause du déclin des populations de homards; (3) ceci a entraîné une explosion des populations d'oursins communs (*Strongylocentrotus droebachiensis*) et, comme conséquence, un broutage destructeur de macro-algues; et (4) le système dénudé qui en est résulté est permanent. Un atelier de travail, organisé par la gestion des pêches, a examiné ces hypothèses à la lumière des travaux présentés et a recommandé des remèdes. On a conclu que la destruction des lits de laminaires dans la baie Ste. Margaret, en Nouvelle-Écosse, était due aux oursins, mais que le mécanisme de déclenchement n'était pas clair. On s'est arrêté aux sources allochthones, à la maladie des laminaires et à l'arrêt de la prédation. Il a été difficile d'évaluer l'ampleur du problème des oursins sur la côte atlantique de la Nouvelle-Écosse et dans la baie de Fundy à cause de l'absence de données historiques à l'est et à l'ouest de la baie Ste. Margaret et du fait que les côtes sud et ouest de Terre-Neuve sont dépourvues de lits de laminaires depuis possiblement plusieurs siècles. On a présenté des données qui laissent supposer que l'augmentation des populations d'oursins le long de la côte de la Californie méridionale résultait d'une prédation excessive de la part d'au moins trois carnivores commerciaux (langouste (*Panulirus interruptus*), labre de Californie (*Pimelometopon pulchrum*) et loutre de mer (*Enhydra lutris*)), ainsi qu'un herbivore (ormeau (*Haliotus rufescens*)). Plusieurs prédateurs naturels des oursins ont été mentionnés pour l'Atlantique nord-ouest, dont quelques-uns, d'importance commerciale (homard, morue (*Gadus morhua*), aiglefin (*Melanogrammus aeglefinus*), plie rouge (*Pseudopleuronectes americanus*), loup atlantique (*Anarhichas lupus*), etc.), avaient subi un déclin; alors que d'autres (crabes, canards, etc.) avaient vu leurs populations diminuer par suite d'autres activités humaines. Il semble que la pyramide alimentaire ait été simplifiée avec, comme conséquence possible, de fortes oscillations du système résultant en importants changements annuels de densité des carnivores. Il serait prématuré de déclarer que l'écosystème des lits de laminaires de la baie Ste. Margaret est ruiné de façon permanente; cependant, on a recommandé que, dans la gestion des ressources halieutiques, on adopte une approche multispécifique/écosystème.

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Introduction

A study was initiated in St. Margaret's Bay, N.S., to assess the trophic relationships in the food chain leading to lobsters. The principal investigator (Mann 1972a) noted a relationship between kelp (*Laminaria* spp.), the green sea urchin (*Strongylocentrotus droebachiensis*), and the American lobster (*Homarus americanus*). Studies on lobster ecology, with the view to resource management, are not new, but Mann felt that the ecosystem approach might be more profitable (Mann 1972c).

His study was begun in 1968 with the assessment of the benthic algal biomass (Mann 1972a) of the Bay. At this time the diversity appeared normal, but the bulk of the biomass was kelp (*Laminaria* spp.). The annual primary productivity contributed to the Bay by seaweeds was 608 g $C \cdot m^{-2}$ (Mann 1972b); the phytoplankton contributed 190 g $C \cdot m^{-2}$ (Platt 1971).

The major herbivore found in this community was the sea urchin *Strongylocentrotus droebachiensis*. Miller et al. (1971) claimed that the production of seaweeds (17 000 kcal $\cdot m^{-2} \cdot yr^{-1}$) (1 cal = 4.1868 J) exceeded the ingestion by herbivores (663 kcal $\cdot m^{-2} \cdot yr^{-1}$) and that food production exceeded that needed to support the lobster population. However, at the time this information was published, destructive grazing of the kelp by urchins was underway. Mann and Breen (1972) speculated "... that heavy exploitation of lobsters may lead to the overgrazing of seaweed by urchins ...." Breen (1974) resurveyed six of Mann's (1972a) transects and noted a 53% reduction in size of the kelp bed. By 1979 the bed had been reduced to 1% of its former size (A.R.O. Chapman, Biology Department, Dalhousie Univ., Halifax, N.S., personal communication).

Thus, between 1968 and 1977 Mann witnessed in St. Margaret's Bay a marked change in what had appeared to be a stable ecosystem. The urchins had appeared to be in equilibrium with the macrophytes but apparently were not (Mann 1977). The system went from one that had supported a luxuriant algal cover to urchin-dominated barren grounds (Mann 1977).

Mann and Breen (1972) suggested first that the commercially important lobster was the "keystone" species in the system and the major predator of the urchin and, second, that the lobster had been reduced to numbers insufficient to control urchin densities. This release from predation allowed the urchins to overgraze the benthic algae (Mann and Breen 1972). They went on to argue that this was likely a stable domain and not cyclic in spite of local anecdotes to the contrary and demonstrations of cycles in California between urchins and kelp. "It is possible we are witnessing a similar cycle in *Laminaria* abundance (similar to California). However, this seems improbable when extensive areas of urchin-dominated barren grounds are reported simultaneously from Newfoundland ... from the Fundy shore .. and from our own samples over about 200 km of coastline in Nova Scotia. The evidence strongly suggests that in these areas the system has moved from a stable domain of attraction (sic) involving dense growths of kelp to another domain involving barren grounds" (Mann 1977). Evans and Mann (1977) go on to claim that "Sea urchins have destroyed kelp beds along many hundreds of miles of Canadian Atlantic coastline and in the same areas lobster stocks have declined." Wharton (1980, and G. Wharton, Biomarine Consultants, Halifax, N.S., personal communication), in recent investigations, claims that both the eastern and southern shores of Nova Scotia's Atlantic coast have little benthic algal cover and that if there is a positive correlation between kelp beds and lobster landings then the latter are bound to decrease in eastern Shelburne County (Fig. 1) due to the presence of urchin-dominated barren grounds.

Most commercial fisheries in Canada are afflicted with large oscillations in annual landings, and fisheries science has not been particularly successful in determining the causal factors (Ketchen 1972). One factor traditionally overlooked has been species interaction; we have concentrated on a single species approach and are only now contemplating a multispecies resource management concept. Mann (1977) was more explicit; he felt resource managers should marry ecosystem theory and population dynamics. He concluded that, had this been done, there may yet be a healthy kelp bed in St. Margaret's Bay.

The coastal waters off both western Shelburne and Yarmouth counties produce 30% of the lobsters in the Maritimes. Many other commercial species are also landed in large quantities, incuding 20 000 t annually of benthic algae (mainly *Chondrus* and *Ascophyllum*) (Pringle and Semple 1980). The development of barren grounds could have a devastating effect on the total fishery through direct reduction in the plant resource, through change in habitat, and through reducing the primary production base of the food chain. Consequently, fisheries management personnel sponsored a workshop (Pringle et al. 1980) in March 1979 to assess principally Mann's (1977) hypothesis "... the explosion of the sea urchin populations was made possible by reduction of predation pressure. An obvious choice of key predator is the lobster." Presented below is a review of the findings and conclusions of this workshop.

Workshop Format

Eighteen background papers were presented at three sessions (Pringle et al.1980). A fourth session, a structured, round-table discussion of topics pertinent to the "Mann hypothesis," was held. The chairman presented statements relevant to the central theme, and discussion followed each statement. The chairman then tabled conclusions based on the discussion. Presented below are the individual statements, a summary of each discussion, and the conclusions reached.

Results

Laminaria

Statement — "There has been a significant decline in *Laminaria* along the Nova Scotia coast in recent years."

The marked decline in the size of the *Laminaria* beds in St. Margaret's Bay (Breen and Mann 1976) was accepted, as it had been well documented since 1968 (Mann 1972a). Wharton's hypothesis (Wharton 1980) that there had been similar declines in *Laminaria* cover west of Halifax was less acceptable. His conclusions were based on present kelp cover as a percentage of suitable substrate availability. His findings

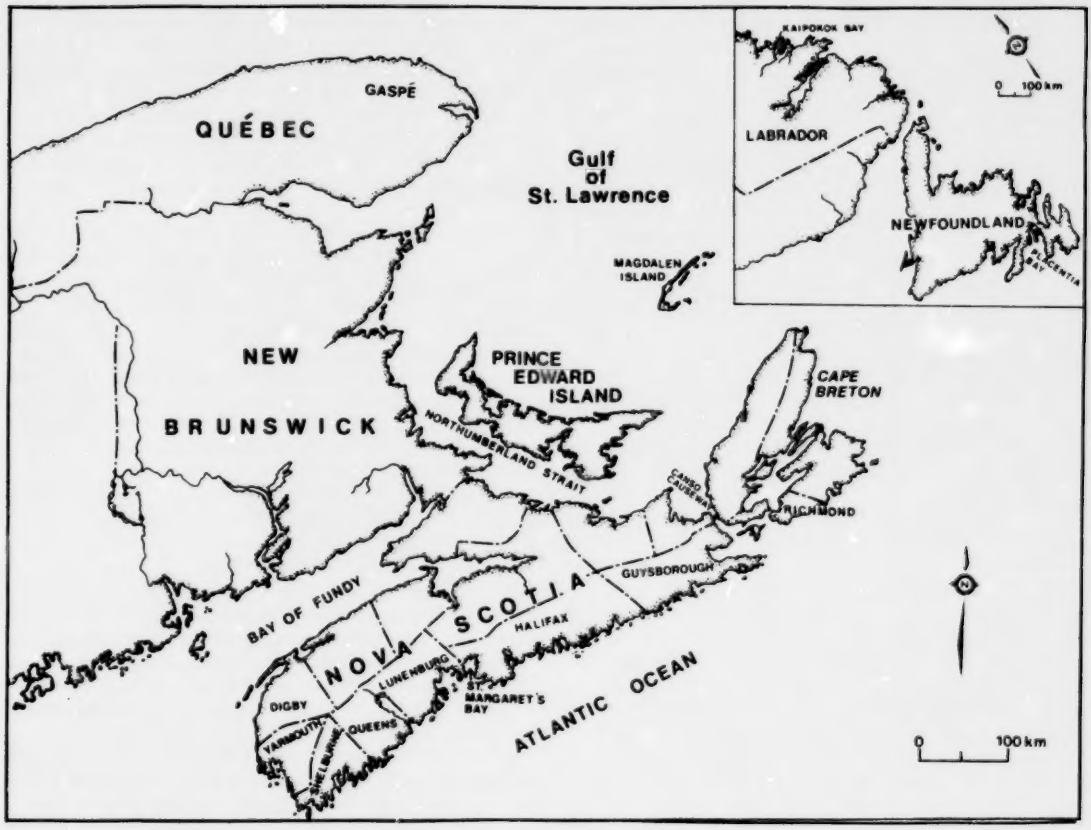

FIG. 1. Atlantic Canada, showing selected counties of Nova Scotia.

were as follows: Lunenburg County, 3.1%; Queens County, 8.8%; and eastern Shelburne County, 11.5%.

It was pointed out by both Himmelman (1980) and Hooper (1980) that much of the Newfoundland coast supports few *Laminaria* beds; the most frequent kelps are *Alaria* and *Agarum*, and they are not abundant. In St. Margaret's Bay, refuge populations of *Laminaria* are found in the surf zone where urchin grazing is not possible (Breen 1980). There are no kelp refuges in Newfoundland, which led Himmelman (1980) to conclude that the urchin-dominated areas "... have not supported *Laminaria* beds in recent history." Similarly, Hooper (1980), for the following reasons, felt *Laminaria* had not been a part of the climax community for hundreds of years: first, the coralline rhodolith layers are metres thick in many areas and one does not find extensive coralline populations as an understory of kelp; and second, sea urchin spines and tests do not increase in the sediments of the recent past.

This discussion pointed out a problem in using the term "urchin-dominated barren grounds," which was believed to have been coined by Lawrence (1975), and others have discussed the concept (see Vadas 1968). These areas in Newfoundland and Nova Scotia are markedly different both in the diversity of flora and fauna and the period of barrenness. Apparently, the urchin-dominated areas in Newfoundland have diverse benthic flora and fauna, whereas this is not the case in St. Margaret's Bay (A. R. O. Chapman personal communication).

Conclusion — "For some areas there has been a significant decline in kelp biomass over the last decade. For many other areas information is lacking, but circumstantial evidence (mainly anecdotal) suggests there has been a general decline, at least east of Cape Sable."

Statement — "The changes in density of *Laminaria* in St. Margaret's Bay are a consequence of abiotic and/or biotic factors."

Caddy (unpublished data) pointed out that domestic sewage in coastal California waters appeared to benefit the urchins more than the kelp; could this be the situation here? This possibility was rejected for St. Margaret's Bay, as apparently nutrient levels are not high (A. R. O. Chapman personal communication). However, St. Margaret's Bay is closed to shellfish harvesting due to high fecal coliform counts (T. W. Rowell, Biologist, Department of Fisheries and Oceans, Halifax, N.S., personal communication). Breen (1974) showed that kelp regenerates on bottom where urchins are excluded by cages. C. Lobban (Department of Science, University of New Brunswick, St. John, N.B., personal communication) pointed out that the latter does not preclude the

possibility some factor(s) may be operating that make(s) the kelp more susceptible to grazing. R. Welsford (Welsford Research Group, Halifax, N.S., personal communication) noted that R. McBride (Associate Professor of Biology, Dalhousie Univ., Halifax, N.S.) had recently discovered a fungal infection that affects local plants of *Laminaria longicruris*. *Littorina* spp. may be the vector of the disease.

Conclusion — "In areas where they have been observed, e.g. St. Margaret's Bay, sea urchins have eaten kelp beds and are the proximate cause of the decline. The data are not sufficient to claim they are the sole cause as there have been environmental changes."

URCHINS

Statement — "Increases in sea urchin abundance along Nova Scotia's Atlantic shores have occurred in recent years."

Discussion on this topic pointed out the lack of information available on both the natural history and population dynamics of local sea urchins. There was little doubt that at certain locations biomass of urchins had increased, e.g. the grazing front in St. Margaret's Bay. However, it was not known whether numbers had increased along the coast: these fronts may be due to emigration and not to recruitment. Unfortunately, neither long-term adult movement patterns nor distribution of the planktonic stages are known. In Russia (J. Himmelman, Laval Univ., Quebec City, P.Q., personal communication), urchin larvae are known to remain planktonic for 2–3 mo. Consequently, local urchin recruitment could be from great distances, given the longshore current patterns of the area. An urchin recruitment pulse following frontal grazing was observed locally (Lang and Mann 1976; Wharton 1980) and in California (Tegner 1980).

Conclusion — "It appears there has been an increase in the biomass of the urchin. Whether there has been an increase in total numbers cannot be answered with the meagre data base."

Statement — "Control of urchin abundance is principally by (a) lobsters, (b) crabs (*Cancer irroratus*), (c) fish, (d) other organisms, and (e) food supply."

Breen and Mann (1976), using a simulation model, suggested that lobsters and crabs could control sea urchin populations under most conditions. Delegates at the workshop were concerned about the lobster densities employed in the model as the latter are largely unknown. It was also felt insufficient weight was given to other predators. Hooper (1980) pointed out a complex predator/prey system off coastal Newfoundland. He identified a minimum of 30 species (Table 1) that prey on urchins of various sizes. Included were commercial groundfish and wolffish (*Anarhichas lupus*). P. Breen (Pacific Biological Station, Nanaimo, B.C., personal communication) noted that wolffish came into St. Margaret's Bay for 3 mo and individuals ate large numbers of sea urchins, but their densities were so low they had trivial effects on the total urchin population. Caddy (unpublished data) noted that wolffish densities dropped in the late 1960s as have most traditional inshore commercial species such as cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). The extent of their past influence on urchin populations is unknown.

Crabs consume urchins (Elner 1980) and they are not commercially harvested in St. Margaret's Bay; however, Pringle (unpublished data) and G. Roach (Biologist, N.S. Department of Fisheries, Halifax, N.S., personal communication) noted that lobster fishermen kill crabs caught in lobster traps as they feel they are competition for lobsters.

Feeding preference experiments found lobsters and crabs had 1:43 and 1:79 preference, respectively, for mussels over urchins (Elner 1980). Each lobster and crab consumed, on average, one urchin per day. The author felt his data did not support the hypothesis that lobsters and rock crabs are a key factor in controlling sea urchin densities. Evans and Mann (1977) showed that lobsters preferred crabs over urchins by 5:1, but they suggested that if urchin densities were markedly higher than those of crabs then more urchins would be eaten.

R. Foreman (Director, Bamfield Marine Station, B.C., personal communication) felt predation on juvenile lobsters and urchins is important but little studied. Similarly, data are lacking on in situ predation rates by lobsters and other predators on urchins as is gut analysis of lobsters. G. Ennis (Research Scientist, Department of Fisheries and Oceans, St. John's Nfld., personal communication) determined that 4–7% of the food in lobster guts was urchin derived.

Tegner (1980) examined the decline of the California kelp beds and the population explosion of urchins. The sea otter (*Enhydra lutris*) had been cited by Mann and Breen (1972) as the predator that controlled urchin populations off coastal California. The otter was eliminated by 1850 and yet there were large, healthy kelp beds up to the late 1940s. During the 1950s, kelp was adversely affected by warm water and water pollution. The urchin explosion was first observed in the early 1960s. She goes on to give good evidence that there was a complex predator/prey system operating in California kelp beds. One urchin predator, the spiny lobster (*Panulirus interruptus*), and a competitor for space and food, the red abalone (*Haliotus rufescens*), are commercially important; the landings for these fisheries peaked in the 1950s. The California sheephead (*Pimelometopon pulchrum*) fishery peaked in the 1960s. She concluded that the competition for space with abalones and the predation by sheephead and lobster may have helped to regulate past populations of sea urchins.

Hooper (1980) noted that urchins have a low tolerance for decreased salinities; he observed mass mortalities off coastal Newfoundland due to a combination of rapid spring thaw, heavy rainfall, and wind. He also noted large numbers of urchins dying of disease, as has been observed off California (Tegner 1980).

Conclusion — "There was insufficient evidence at present to claim that lobsters were the primary predators of sea urchins and that urchin populations exploded due to a release from predation by lobsters."

Statement — "The present abundance of sea urchins and lowered densities of *Laminaria* in St. Margaret's Bay is a permanent phenomenon."

Empirical data go back 10 yr for St. Margaret's Bay (Breen and Mann 1976), insufficient time to observe cycles. A large amount of anecdotal evidence was presented suggesting that *Laminaria* beds are ephemeral. D. Scarratt (St. Andrews Biological Station, St. Andrews, N.B., personal communication) rarely observed kelp in the northern portion of Northumberland Strait, where it now apparently is a nuisance factor to the lobster fishermen (R. Henry, Provincial Depart-

TABLE 1. Observed sea urchin predators in Newfoundland waters.

	Sea urchin size			
	Larvae	Small (5 mm)	Medium (5+ to 25 mm)	Large (>25 mm)
Predators	*Cyanea* spp.	*Tealia* spp.	*Tealia* spp.	*Anarhichas* spp.
	Pleurobrachia spp.	Pleuronectidae	*Anarhichas* spp.	*Solaster* spp.
	Ophiopholis spp.	Pholidae	Pleuronectidae	*Tealia* spp.
	Metridium spp.	*Ulvaria subbifurcata*	*Solaster* spp.	*Harus argentatus*
	Haliclonidae	*Cancer* spp. (juvenile)	*Gadus morhua*	*Homarus americanus* (mature)
	Boltenia spp.	*Hyas* spp.	*Leptasterias* spp.	*Cancer* spp.
	Anthozoan medusae	*Homarus americanus* (juvenile)	*Cancer* spp.	
		Solaster spp. (juvenile)	*Harus argentatus*	
		Gadus morhua (juvenile)	*Homarus americanus*	

ment of Fisheries, Fredericton, N.B., personal communication). Similarly, G. Roach (personal communication) claimed that fishermen of both Richmond and Guysborough counties have noticed a synchronous decline in kelp and lobster and an increase in urchins. They now find signs the reverse is true. Breen (1980) outlined similar anecdotal evidence. The only long-term data for kelp might be old admiralty charts which often included kelp beds (D. Pace, Occam Marine Technologies, Armdale, N.S., personal communication).

Hooper (1980) and Himmelman (1980) both noted that urchin-dominated areas appeared to be a permanent mode for many areas off coastal Newfoundland. Consequently, it could be argued that the *Laminaria* community observed in St. Margaret's Bay was a unique phenomenon and the present urchin-dominated beds are the more normal mode.

Tegner (1980) outlined cyclic patterns between urchins and kelp off California which had periods of 12 yr. Geomorphology was important in these cycles. Beds in rugged terrain were occupied by spiny lobsters and sheephead, which tended to keep the urchin population under control; hence, these populations did not oscillate. Kelp populations on flat bottom with no lobsters or sheephead oscillated with urchin abundance.

Conclusion — "There appears to be a degree of cyclicity between populations of urchins and kelp in certain areas of the northwest Atlantic, based on anecdotal evidence only. It would appear the present situation in St. Margaret's Bay may be a little more severe but it does not imply that it is permanent."

Statement — "Declines in lobster and inshore fish abundance along Nova Scotia's eastern shore have occurred in recent years. For lobsters, this is due to changes in environmental factors,overfhishing or other predators, food shortages, or lack of cover."

Changes in environmental factors were shown to relate to fluctuations in lobster landings along the Quebec coast (Sutcliffe 1973). Sutcliffe showed a 9-yr lag between landings and the St. Lawrence River discharge volume. D. Robinson, (Biologist, Department of Fisheries and Oceans, Halifax, N.S., personal communication) feels this is an effect but only for annual fluctuations, not for the long-term decline in lobster stocks.

Recruitment overfishing was the most strongly supported factor for the decline in lobster landings (A. Campbell, St. Andrews Biological Station, St. Andrews, N.B., personal communication). The current size limit of 81 mm carapace length is well below the average size of female maturity, which is 100 mm carapace length (Stasko and Campbell 1980).

The decline in stocks of Guysborough and Richmond counties brought about the introduction of larger traps. This permitted the capture of jumbo lobsters, possibly accelerating the final decline in landings (G. Roach personal communication). Fishing pressure was reduced from 120 fishermen to 20 for this area. There appears to be an increase in juvenile (less than 81 mm) lobsters, which suggests that a recovery of stocks may be occurring. However, areas where catches have been stable have recently shown declines, e.g. Lobster Bay, particularly inshore (Stasko and Campbell 1980).

In general, Robinson (1980) suggested that fishermen are a far more efficient predator today than in the past due to the introduction of radar, larger boats, and hydraulic hauling gear. Robinson (1980) also noted that the introduction of market size limits in 1933 (22.5 cm total length) removed fishing pressure on young recruits and resulted in stabilization of the catch until recently (Robinson 1980).

There was no evidence food supply was a limiting factor. Declining lobster populations would quickly stabilize any food to lobster biomass imbalance.

The importance of *Laminaria* and other benthic plant species as protective cover for juvenile and mature lobsters has not been directly investigated. Indirect information comes from benthic studies investigating other questions. For instance, in studies of lobster feeding, "We found that on those *Chondrus* beds (Gulf of St. Lawrence) lobsters tended to move onto them as the season (summer) approached, and tended to vacate as winter approached ... we seem to find most of our new set of lobsters 6–9 mm carapace length in the 4–8 fathom range" (D. Scarratt personal communication). This was confirmed by divers doing algal studies in this area (J. Pringle unpublished data). Studies of scallop beds below *Chondrus* beds found large numbers of lobster less than 20 mm carapace length (G. Jamieson, Pacific Biological Station, Nanaimo, B.C., personal communication). As well, in Placentia Bay an abundance of juvenile lobsters (20 juveniles per diver hour) were reported for areas devoid of macroalgae (J. Carter, Martec Consulting Ltd., Halifax, N.S., personal communication). Coastal British Columbia macrophyte beds were reported to provide complex habitats for both prey and predator (R. Foreman personal communication); juvenile crabs in particular were found in rocky, seaweed-dominated areas. South African studies found "... large numbers of

invertebrates in the holdfasts of kelp and (but) it is difficult to find the young lobsters there too (in the kelp beds)" (J. Field, Zoology Department, University of Capetown, Rondesbosch, South Africa, personal communication). D. Scarratt (personal communication) suggested that the habitat area increases for lobster in a kelp bed.

The relatively high and stable catches of lobsters in southwest Nova Scotia may be due to upwelling of nutrient-rich waters which may provide the high productivity required to prevent the decline in landings experienced on the eastern shore. By contrast, nutrient levels along the southeastern shore are low (Chapman and Gagné 1980). As well, current patterns may supply larval recruitment from offshore banks in inshore southwest Nova Scotia (Stasko and Campbell 1980), which likely does not occur along the eastern shore.

Conclusion — "Recruitment overfishing of lobsters appears to have been a major factor in the decline in landings. No overwhelming evidence is available that environmental factors, food, or plant cover were important factors in population declines."

Discussion

There is an unfortunate lack of quantitative, ecological data for subtidal communities along northwestern Atlantic shores. MacFarlane (1952) surveyed commercially important, subtidal plant populations for the shores of Shelburne, Yarmouth, and Digby counties; Edelstein et al. (1969) did distributional studies off Halifax County (Fig. 1). However, it was not until Mann's (1972a) timely study of St. Margaret's Bay that quantitative data were available east of Shelburne County. The ecosystem as it existed 25–100 yr ago is unknown. During this period lobster, groundfish, and pelagic fish have been extensively harvested. Furthermore, along these shores human densities have increased, limited areas have been industrialized, and major ecological perturbations, such as the Canso Causeway (Fig. 1), have taken place. Given the above, it was difficult to accept Mann's hypotheses that (1) the lobster is a keystone predator of the kelp bed ecosystem, and by overharvesting the lobster it has caused *Laminaria* densities to decline drastically along hundreds of miles of the western Atlantic shore (Evans and Mann 1977), and (2) that urchin-dominated barren grounds constitute a stable ecosystem (Mann 1977).

There is little doubt the kelp bed ecosystem observed by Mann (1972a) in the late 1960s is all but gone. We know that similar kelp bed ecosystems are not present on much of the available substrate along coastal Guysborough, Halifax, Lunenburg, Queens, and Shelburne counties (Wharton 1980); but evidence they were there in the past is lacking. This gap in the data base is particularly unfortunate, as Hooper (1980) and Himmelman (1980) noted that much of the coast of Newfoundland, Labrador, and Gaspé is similarly lacking this kelp bed ecosystem. They presented good evidence that these coasts may never have supported kelp beds as observed by Mann (1972a) in St. Margaret's Bay. We were also presented with anecdotal evidence going back to 1851 (Breen 1980) that urchin populations periodically overgrazed large stretches of the subtidal.

The urchin-dominated areas of Newfoundland and Nova Scotia are different in structure even though kelp is not present in either. Off Newfoundland, coralline communities are well developed, some with rhodoliths metres thick. This apparently is not the case off Nova Scotia (St. Margaret's Bay) where A. R. O. Chapman (personal communication) noted that on average, coralline plant density was 1 m $^{-2}$. Thus, there is the possibility the southern Newfoundland coast was perturbed many years ago and the Nova Scotia coast only recently, both flipping from a productive kelp bed ecosystem to a less productive coralline/urchin system. Off Pt. Loma, California, the kelp beds were reduced to 0.05 km^2 but now measure 5.1 km^2, showing the resiliency of *Macrocystis* beds (Tegner 1980). Foreman (1977) noted a similar recovery in *Nereocystis* beds off British Columbia. This may not necessarily happen, however, off Nova Scotia.

Given that something has perturbed the system, it would be appropriate to learn its nature and, if possible, take remedial action. If it is disease, as affected eelgrass along the northwest Atlantic, it would likely have to run its course. If it is allocthonous then the source could be curtailed. If, however, it is due to the commercial overharvesting of carnivores then a multispecies resource management program should be implemented immediately in an attempt to "stem the tide."

Tegner (1980) presented a well-documented argument outlining poor resource management as the major cause of destructive grazing by urchins off California. She suggested that commercial overharvesting of the spiny lobster, the red abalone, the California sheephead, and the otter, extreme warm waters during the late 1950s, and allochthonous substances from industrial Los Angeles and San Diego led to kelp destruction, not just the demise of the otter as suggested by Leighton et al. (1966). Similarly, the overgrazing of macrophytes in St. Margaret's Bay was probably not due solely to commercial overharvesting of the lobster. The density of many other commercial species has been reduced markedly.

It is a well-known ecological concept that the simpler the trophic pyramid the more productive the system. However, organization theory shows this leads to a system with wild annual oscillations in population numbers (Watt 1968). The original kelp bed ecosystem, as it may have existed 400 yr ago, would have been more complex and hence more stable than that which was observed by Mann (1972a) in St. Margaret's Bay.

During the 17th century, man began extensive fishing off coastal Nova Scotia and Newfoundland, taking large catches of haddock, cod, halibut (*Hippoglossus hippoglossus*), pollock (*Pollachius virens*), etc., all known urchin consumers at some stage of their life cycle. Lobsters were first fished commercially during the 19th century, and by the turn of the 20th century the point of maximum sustainable yield had been surpassed (Robinson 1980). Catch per unit effort (CPUE) data are not available for this period, but if landings reflect lobster densities then there were periods between 1912 and 1924 when densities were comparable to those of present day.

In summary, what may have happened was that a complex, kelp bed ecosystem was transformed into a simple system through the overharvesting of a number of fish species. Consequently lobster and crab over the last 50–70 yr were the major nearshore carnivores. Being a more simple system small perturbations such as a single-year recruitment failure of lobster, along with intense commercial pressure, allow wild oscillations.

The above suggests a "boom and bust" fishery that has not been managed for maximum sustainable yield. What has been concluded for California (Tegner 1980) likely holds for the northwest Atlantic: the overgrazing by urchins is due to the removal of a number of carnivores, the lobster being only one of them. Consequently, Mann's hypothesis of the lobster as a keystone predator is rejected. However, his ecosystem approach to resource management is not. What apparently is required to maintain a stable ecosystem is a high degree of stability at the carnivore level which would encourage stability at the herbivore level "... by damping the oscillations of increasing amplitude inherent in a predator/prey system with delayed negative feedback" (C. S. Holling in Watt 1968). Thus, to manage the resource for maximum sustainable yield, all trophic levels and predators must be considered. This points to Watt's (1968) contention that most resources have rarely been managed scientifically "... even in instances where it was generally considered that this was being done." Watt (1968) concluded that management practices must be carefully conceived regarding basic ecological principles if productivity and stability are to be maintained at optimum levels. Due to the complexity of ecosystems, with their attendant physical and chemical parameters and the difficulty in defining optimum management strategy, one is forced to resort to complicated systems analysis and simulation procedures.

Recognizing the complexity of this problem and the large number of data gaps, implementation of coordinated programs of experimentation and observation are necessary. However, the acquisition of usable data from such studies ranges from 1 to 10 yr from initiation, depending on generation time of the study organism and rates of colonization and succession. Within this time frame the commercial inshore fishery could collapse completely (many fishermen claim it has already). We must act upon our present state of knowledge. The most obvious area for potential correction is recruitment of lobsters: the first step would be an increase in size of first capture to the age of first maturity. At present, the number of urchins in certain areas is so great it will require more than 1 yr of high predator recruitment to reduce urchin densities significantly. Hence, destructive grazing of macrophytes will continue for some time beyond the recovery of predator populations. Remedial measures must be taken to reduce urchin densities where macrophyte destruction is transitional to a barren mode. Development and implementation of economical restoration methods can be instituted in chronic barren grounds.

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Comparison of Length Distributions of Combined Catches of all Demersal Fishes in Surveys in the North Sea and at Faroe Bank

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Aggregated length distributions of all fish species obtained from groundfish surveys in the North Sea and at Faroe Bank are displayed. These distributions show interesting regularities and hence may be a useful aggregated description of the general situation in a fisheries area. The comparison of the northern North Sea results and those from Faroe Bank show differences which would be consistent with the different fishery regimes in the two areas.

Key words: length distributions, multispecies, North Sea, Faroe Bank, aggregated

POPE, J. G., AND B. J. KNIGHTS. 1982. Comparison of length distributions of combined catches of all demersal fishes in surveys in the North Sea and at Faroe Bank, p. 116–118. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

Les auteurs présentent les distributions des longueurs combinées de toutes les espèces de poissons capturés au cours de relevés des poissons de fond dans la mer du Nord et sur le banc des Féroé. On y observe une intéressante régularité, et il est à souhaiter que ces distributions soient utiles à décrire la situation générale dans une aire de pêche. Quand on compare les résultats du nord de la mer du Nord avec ceux du banc des Féroé, on trouve des différences qui correspondraient à des régimes de pêche différents dans les deux régions.

Introduction

Annual recruitment to stocks of arctic and temperate fishes is typically highly variable. In single species assessments this variability of recruitment leads to predictions of new steady-state yield and stock biomass that are essentially averages. The problem is compounded in multispecies assessments because changes in recruitment levels to a stock change both the predictions for the stock in question and also the predictions about stocks with which it interacts. Thus, predictions of stock biomass or yield from a temperate or arctic multispecies fishery must be regarded as average values where the averaging period might be as much as 20 yr. In practice such predictions are difficult or impossible to test against the future behavior of the fishery. It would, therefore, seem wise to consider what predictions can be made that might allow testing in a suitably short time. Obviously such a prediction would need to be about some robust feature of the fisheries system.

Biomass at length distributions have been shown by Sheldon et al. (1977) to be conservative features of marine planktonic communities. It is interesting to ask if such size distributions show regularities in exploited demersal fish populations. Such distributions might indicate something of the overall state of a fisheries area, particularly if they could be compared over the course of development of a fishery or of a fisheries management strategy. Comparisons between areas and over time might also shed light on the effects of different management regimes. To stimulate such investigations we examined such distributions from two regions.

Groundfish Survey Data

Since 1977, groundfish surveys have been carried out in the North Sea by RV *Cirolana* using a Granton trawl. On these surveys the length distribution of each fish species caught at each trawl station was recorded. These species length distributions were combined to give the average numbers at each length for all fish species combined. These annual average distributions are shown in Fig. 1 as numbers at length (on a logarithmic scale) from the 1977, 1978, and 1979 surveys.

There is considerable regularity of the numbers at length in each year, the numbers in any one centimetre grouping rarely varying between years by more than a factor of two, although the total range of the distributions covers more than four orders of magnitude. It seems therefore that the length distribution of the demersal catch made by the Granton trawl is rather consistent, despite the well-known variability of the year-class strength of individual species and the bimodal nature of their length distributions.

It might be expected that these distributions would change as a result of changes in fisheries management and it might be useful to contrast them with surveys of the North Sea made in earlier years by the Marine Laboratory, Aberdeen. At present the only comparison available to the authors is with the 1971 survey at Faroe Bank reported by Jones and Pope (1973). Figure 2 shows the average numbers at length per station from the Faroe Bank survey (stations shallower than 200 m only) and from the northern North Sea stations (ICES Region IVa) of the 1978 groundfish survey. The comparison of length distributions shows striking differences between the two

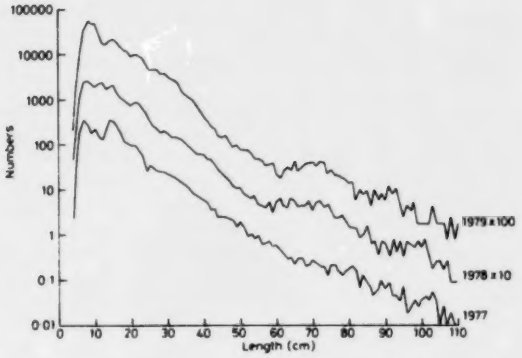

FIG. 1. Average numbers at length per station of all demersally caught fish from North Sea groundfish surveys.

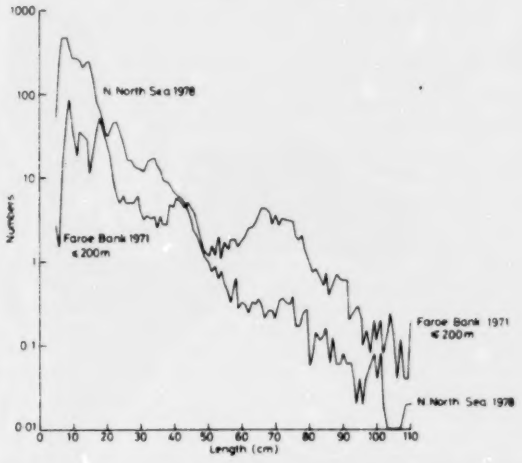

FIG. 2. Average numbers at length per station from the Faroe Bank and northern North Sea groundfish surveys.

areas, the northern North Sea having far fewer large fish and far more small fish. What is not clear is the extent to which the differences reflect the different commercial fishing patterns in the two areas or actual physical differences between the two areas. The northern North Sea (ICES fishing area IVa) was chosen for comparison because it is more similar to Faroe Bank in depth and in species composition than more southerly areas of the North Sea. The species list from the Faroe Bank survey contains only one species, spotted catfish (*Anarhichas minor*), not found in one or other of the 1977–79 surveys in the northern North Sea stations. The species list from these northern North Sea stations contains 63 species or species groups, of which 31 species were not found in the 1971 survey at Faroe Bank. Twelve of these 31 species might reasonably be expected to be found on Faroe Bank in an extended survey series. These 31 species accounted for 23% of the weight of fish caught in the northern North Sea stations in 1978. Most of this weight (21% of the total catch in the northern North Sea stations) was taken from only four species. These were whiting (*Merlangius merlangus*), pollack (*Pollachius pollachius*), mackerel (*Scomber scombrus*), and *Raja radiata*. All these are comparatively large species and in fact in 1978 the average length of the non-Faroe Bank species was somewhat higher than the average length for all northern North Sea fish. It seems therefore that these extra species found in the North Sea survey do not explain the differences in length distributions observed. Comparison of the cumulative biomass at length from the North Sea surveys with that from the Faroe Bank survey underlines the difference (Fig. 3). In the North Sea 50% of the biomass occurs below

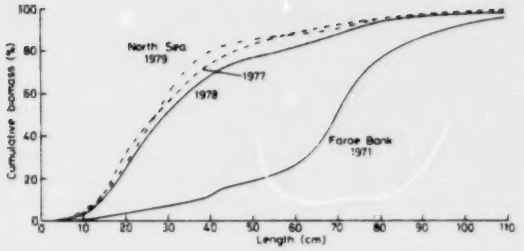

FIG. 3. Cumulative biomass at length curves for the North Sea, 1977–79, and for Faroe Bank, 1971.

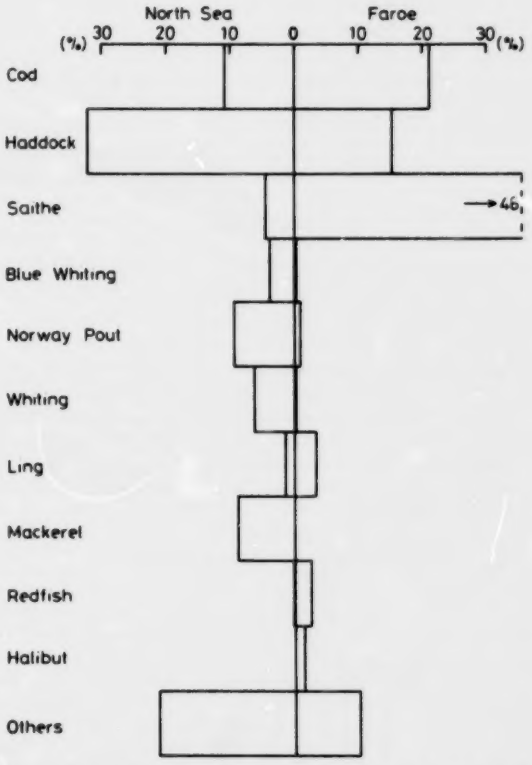

FIG. 4. Relative abundance by weight of species at Faroe Bank and the northern North Sea.

30 cm; in the Faroe Bank survey 50% of the biomass occurs below 70 cm (a length that would cover between 85 and 90% of the biomass in the North Sea surveys). These differences are partly due to seasonal factors. The Faroe survey was made in June before the 0-group fish descend to the bottom, whereas the North Sea survey was made in August to September after many of the fish had descended. This would therefore tend to depress the level of the 50% biomass point for the North Sea survey but, because fish of less than 15 cm account only for 12–13% of the biomass, the effect would not be large. With the less than 15 cm fish omitted the 50% biomass point might increase to 33 cm at most in the North Sea survey results. The difference in the distribution of cumulative biomass in the two areas is therefore considerable even when 0-group fish are excluded from the analysis.

Apart from the differences in the size distribution between Faroe and the North Sea, the relative importance of the main species is different. Figure 4 shows the percentage of the total survey catch for various species at Faroe Bank in 1971 and in the northern North Sea in 1978. Clearly, the larger predacious species such as cod, saithe, ling, and halibut are relatively more abundant at Faroe Bank.

Discussion

It is tempting to speculate that the differing size distributions at Faroe Bank and in the North Sea result largely from the different patterns of exploitation that have been imposed on the two areas. The mesh size in force at Faroe Bank in 1971 was 110-mm manila whereas the mesh size for the North Sea in 1977–78 was 80-mm manila. Moreover, the extensive small mesh fisheries for industrial fish in the North Sea in this period effectively makes this figure lower. It would seem reasonable to suppose that the reduced numbers of large fish in the North Sea result from the intensity of fishing. Whether the relatively greater number of small fish in the North Sea is a result of a reduction in predation is less clear. It is probable that, in part, the comparatively low number of fish in the 5- to 15-cm band at Faroe results from the time of year the survey was carried out. The fact remains, however, that the 25- to 35-cm fish are also reduced compared with the North Sea.

These results raise two questions. First, how are size distributions affected by changes in the fishing pattern and intensity? The data given here cannot answer this question but it is possible that the extensive time series for the North Sea reported by Richards et al. (1975) or the Georges Bank survey (Grosslein 1971) might yield interesting insights into the changes of size distribution with fishing pressure. Second, how should the size spectrum of fish be most effectively exploited? Should fishing pressure be an increasing function of size, a decreasing function of size, or some discontinuous function?

Apparently, size distributions of combined catches of fishes in a demersal assemblage may be a useful tool in the study of multispecies fisheries. Retrospective analyses of existing time series of groundfish survey data might give insights for construction of simplified multispecies models. Size distributions might also be a useful way of condensing the output of more complex simulation models.

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Multispecies, Multistock Aspects of Pacific Salmon Management

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HEALEY, M. C. 1982. Multispecies, multistock aspects of Pacific salmon management, p. 119–126. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

The Pacific salmon (*Oncorhynchus* spp.) fisheries along the west coast of North America represent one of the most complex of resource management systems. Five species of anadromous salmonids contribute to the fishery. The number of stocks (defined as the members of a particular spawning population) of each species ranges from 300 for sockeye (*O. nerka*) and chinook (*O. tshawytscha*) to 970 for coho (*O. kisutch*) for a total of 3150. Furthermore, each stock can be composed of several discrete brood lines and life history types. The intermingling of species and stocks is such that there are virtually no single stock fisheries, and some fisheries involve mixtures of several species and hundreds of stocks. Four principal types of gear are used in the fisheries, and three principal user groups participate. The combined power of the fishing fleet is sufficient to fish out most stocks within a single season, and each user group is politically active in seeking a bigger share of the allowable catch. About eight political jurisdictions, each with a vested interest in salmon, also influence the process of management. The conceptual basis of current salmon management is stock–recruitment theory. The concept is useful qualitatively, but empirical data do not permit a precise quantitative application of the theory. The Schaefer model, which is the basis of some recent work on multispecies fishery theory, also provides a poor quantitative fit to salmon data. It is concluded that the developing theory of multispecies fisheries will be of limited value in quantitative management of salmon fisheries, and there is need to pursue ways to improve the decision-making process in the face of continuing uncertainty about population parameters and continuing pressure from user groups for a bigger total catch and a bigger share of the catch.

Key words: multispecies, multistock, Pacific salmon, management

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Les pêcheries de saumons du Pacifique (*Oncorhynchus* spp.) le long de la côte occidentale de l'Amérique du Nord représentent un des systèmes de gestion les plus complexes. La pêche est alimentée par cinq espèces de salmonidés anadromes. Pour chaque espèce, le nombre de stocks (définis comme étant les membres d'une population reproductrice particulière) varie de 300 dans le cas des saumons nerka (*O. nerka*) et chinook (*O. tshawytscha*) à 970 dans celui du saumon coho (*O. kisutch*), pour un total de 3150. De plus, chaque stock peut comprendre plusieurs lignées reproductrices et types de cycles biologiques distincts. Les espèces et les stocks se mélangent à un degré tel qu'il n'existe pratiquement pas de pêche de stocks uniques et que dans certains cas on exploite un mélange de plusieurs espèces et de centaines de stocks. Trois groupes principaux d'utilisateurs récoltent cette ressource au moyen de quatre principaux types d'engins. La capacité combinée de la flottille de pêche suffirait à récolter entièrement la plupart des stocks en une saison, et chaque groupe d'utilisateurs exerce des pressions politiques afin de s'approprier une plus grande part des prises admissibles. Il y a en outre huit juridictions politiques, chacune avec un intérêt matériel dans la pêche du saumon, qui influent également sur le processus de gestion. À l'heure actuelle, la gestion du saumon est fondée sur la théorie stock–recrutement. C'est un concept qualitativement utile, mais les données empiriques ne permettent pas une application quantitative précise de la théorie. Le modèle de Schaefer, à la base de récents travaux sur la théorie des pêches d'espèces multiples, s'ajuste mal quantitativement aux données sur le saumon. Nous concluons que la théorie des pêches d'espèces multiples en voie d'élaboration aura une valeur limitée dans la gestion quantitative de la pêche des saumons. On devra continuer à chercher des moyens d'améliorer le processus décisionnel face à l'incertitude qui existe toujours concernant les paramètres de population et aux pressions des groupes d'utilisateurs qui veulent se voir accorder des prises totales plus fortes et une plus grande part des prises.

Introduction

The salmon fisheries along the west coast of North America represent one of the most complex of resource management systems. Much of this complexity stems from the multispecies, multistock nature of the fisheries. The purpose of this report is to describe the salmon fisheries, and to consider how the developing theory of multistock fisheries, as well as other conceptual aids to decision making, can assist in the management of these fisheries.

In this discussion I shall draw examples from salmon fisheries along the coast of British Columbia, Canada. I shall also emphasize the practical aspects of managing the fisheries. As is usually the case, there is a considerable gap between theory

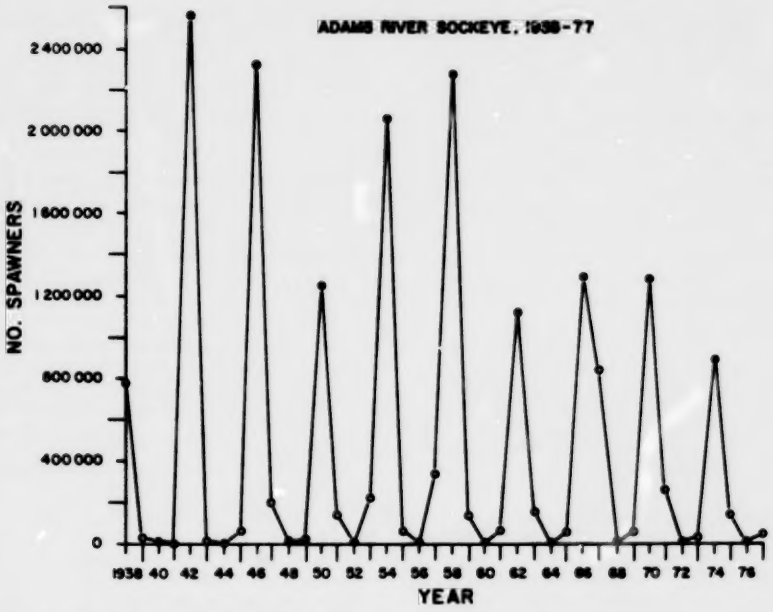

FIG. 1. Cyclic dominance in Adams River sockeye salmon as shown by spawning escapement. Data are from Larkin (1971) and International Pacific Salmon Fisheries Commission annual reports for 1970–77.

and practice in the management of salmon fisheries, and it is important to ask whether the theory is developing in a way that will have practical application.

The Salmon Fisheries

The foundation of the fisheries is the five species of Pacific salmon (sockeye, *Oncorhynchus nerka*; pink, *O. gorbuscha*; chum, *O. keta*; coho, *O. kisutch*; chinook, *O. tshawytscha*) found on the west coast of North America. All five species are anadromous, spawning in freshwater in the autumn and winter, and migrating to sea as juveniles where most of their growth occurs. In the sea all species range widely along the coast and out into the North Pacific for 1 yr or more. As maturing adults they return along specific migration routes to their natal streams, spawn, and die. In consideration of their general life history pattern, I define a "stock" of salmon as the members of a particular spawning population (Paulik et al. 1967; Ricker 1972). All such populations are genetically isolated to a considerable degree. It is a common supposition, stimulated by discussions such as those of Calaprice (1969), Raleigh (1967, 1971), and Ricker (1972), that each stock has evolved unique genetic adaptations. This supposition, for which there is, as yet, no general empirical demonstration, underlies some of the present concern about multistock salmon fisheries.

Each of the five species has a characteristic life history pattern with variations. Sockeye, for example, normally spawn in rivers tributary to a lake, and young sockeye spend a year or more rearing in the lake before migrating to sea. The young of a few races, however, rear in river channels or migrate to sea in their 1st yr of life. Sockeye return to spawn in their 3rd–6th yr at weights of 2–3 kg, depending on the particular spawning stock, their length of freshwater residence, and so on. An often reported feature of sockeye stocks is that some show cyclic dominance among brood lines (Ricker 1966). The Adams River stock in the Fraser River system shows a typical 4-yr cycle (Fig. 1) (Ward and Larkin 1964; Larkin 1971). The 1902 brood line is the dominant line in the Adams River. The 1903 line is called the subdominant line, but only rarely has the 1903 line rivaled the 1902 line in abundance. The 1901 and 1904 lines have been continuously 1–2 orders of magnitude less abundant than the dominant line.

There are about 300 stocks of sockeye in British Columbia. The total population is currently about 5–12 million depending largely on the size of the Fraser River run (Aro et al. 1977).

Pink salmon, in contrast with sockeye, migrate to sea as fry shortly after emerging from the spawning gravels in spring. Pink salmon invariably return to spawn in their 2nd yr at a weight of about 2 kg. Pinks are unique among Pacific salmon in having such a fixed life span. This does not necessarily make them an easy species to manage. Pink salmon can show cyclic dominance in the extreme. In the Fraser River–Puget Sound area, for example, the even-year brood line is virtually absent whereas the odd-year brood line numbers in the millions. On the north coast of the Queen Charlotte Islands the opposite situation prevails, with even-year brood lines generally abundant and odd-year lines generally scarce (Fig. 2) (Neave 1962). Even- or odd-year brood lines are known to dominate in other regions of the North Pacific, and dominance

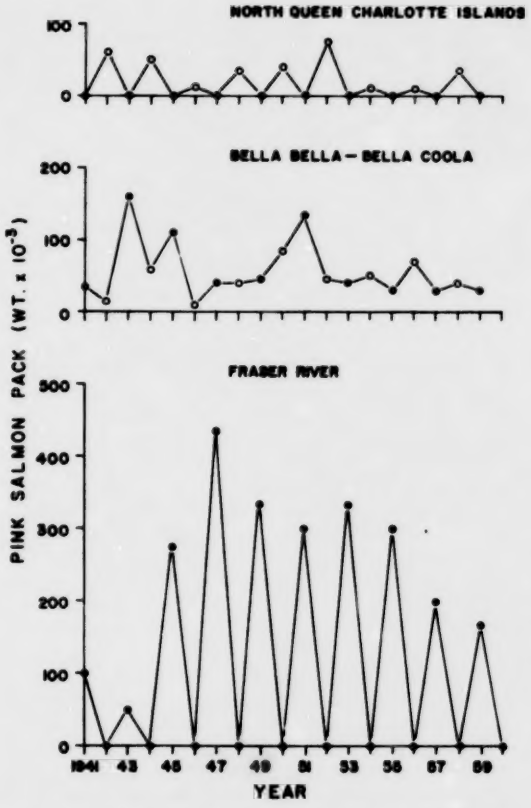

FIG. 2. Cyclic dominance among pink salmon as demonstrated by the salmon pack from three regions of the British Columbia coast. Adapted from Neave (1952).

has been observed to shift from one brood line to another in certain stocks (Royce 1962; Ricker 1962).

There are about 700 stocks of pink salmon in British Columbia. The total population is around 10 million in odd years and 25 million in even years (Aro et al. 1977).

Chum salmon, like pink salmon, migrate to sea as fry shortly after emerging from the spawning gravels. During their early sea life, chum are similar in their behavior and general ecology to pinks, with the exception that chum will rear in estuaries whereas pinks apparently do not (Healey 1980a). Chum return to spawn in their 3rd–5th yr weighing 4–6 kg.

There are about 880 stocks of chum in British Columbia. In contrast with pink and sockeye, where only a few large stocks contribute most of the catch (Aro and Shepard 1967), many small stocks of chum contribute most of the catch. Protecting the many small spawning populations of chum while permitting the effective harvest of surplus production poses some special problems for the fishery manager. To make matters worse, British Columbia chum stocks have shown wide and unpredictable fluctuations in abundance (Fig. 3). The total population of chum has ranged about 2–10 million in recent years (Aro et al. 1977).

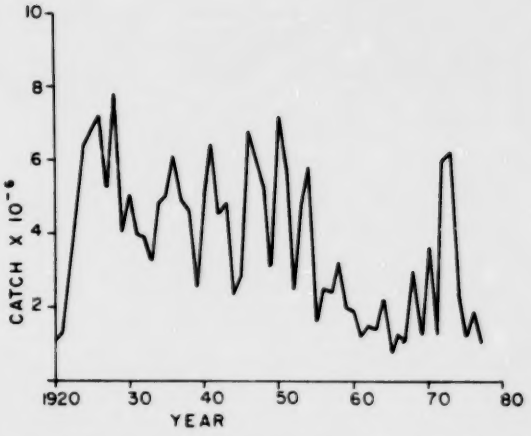

FIG. 3. The commercial catch of chum salmon in the coastal waters of British Columbia, 1920–78.

Coho normally spend a year or more in freshwater before migrating to sea, although a few migrate to sea during their first summer. Coho usually spend their freshwater life in a river or stream, although some also rear in lakes. Most coho in British Columbia return to spawn in their 3rd yr weighing 2–4 kg, a few return to spawn in their 4th yr, and some males also mature precocially in their 2nd yr.

There are about 970 stocks of coho in British Columbia. As with chum, many small spawning populations contribute substantially to the total production. The total population of coho in British Columbia is about 4 million (Aro et al. 1977).

Chinook are the least abundant of the five salmon species on the British Columbia coast. They also have the most variable life history pattern, at least during their early life (Healey 1980a, b). Some chinook go to sea as recently emerged fry, others as fingerlings after 2–3 mo in freshwater, and some after a year or longer in freshwater. The length of time young chinook spend in freshwater tends to increase from south to north. Sockeye and coho also show this trend (Hart 1973; Godfrey 1965). In British Columbia, chinook that go to sea after 2–3 mo of freshwater residence are the most common type. Those which migrate as fry, however, or as yearling or older smolts are abundant in some systems. Chinook return to spawn in their 3rd–6th yr weighing 5–20 kg.

There are about 300 stocks of chinook in British Columbia. For most of these, fewer than 5000 fish escape upstream to spawn. The total population is about 1–1.5 million.

All five species of Pacific salmon range widely in the North Pacific during their ocean residence (Hart 1973). For British Columbia stocks the trend is to migrate north during the spring and summer, and then south in the autumn and winter (Royce et al. 1968). In general, British Columbia stocks do not range much west of 175°W or south of 45°N. The north–south distribution of stocks in the ocean tends to correspond to the north–south distribution of their natal streams. There is some separation of stocks in the ocean, therefore, but the degree of intermingling is considerable, both at sea and during the spawning migrations when the stocks are most intensively fished. During their ocean residence, and during parts of their

TABLE 1. Elements in the salmon fishing system.

		N
Political jurisdictions	Japan	
	USA	
	California	
	Oregon	
	Washington	8
	Alaska	
	Canada	
	British Columbia	
User groups	Commercial fishermen	
	Recreational fishermen	3
	Subsistence fishermen	
Gear		
	Troll	
	Seine	
	Gill net	5+
	Sport	
	Various subsistence	
Species		
	Sockeye	
	Pink	
	Chum	5
	Coho	
	Chinook	
Spawning stock	300 + sockeye	
	700 + pink	
	880 + chum	3150+
	970 + coho	
	300 + chinook	
Brood line	4 + sockeye	
	2 pink	
	4 + chum	17+
	3 + coho	
	4 + chinook	
Life history type	3 + sockeye	
	1 pink	
	1 + chum	12+
	3 + coho	
	4 + chinook	

return migration, British Columbia salmon stocks also intermingle with U.S. and Asian stocks.

Considering only the salmon stocks of British Columbia origin, we have a system that involves five species and is comprised of some 3150 spawning populations or stocks (Table 1). Each stock is composed of several partially independent brood lines, two for pinks, up to four to five for sockeye and chinook. Each brood line may comprise fish of several different life history types which could be genetically independent. No one supposes that all of the potential interactions that might occur among the thousands of stocks, brood lines, and life history types are important to the management of the fishery. There are many possibilities for complex and unsuspected interactions, however, and this introduces uncertainty into predictions of stock behavior. Parker (1971), for example, implicated predation by coho on pink and chum fry as reinforcing species-specific characteristics and possibly influencing the productivity of these two species.

The fish themselves are only one component of the many faceted fishery system. Other facets include gear types, user groups, and political jurisdictions. On the British Columbia coast, four main types of gear are engaged in the fishery: purse seine, gill net, commercial troll, and sport troll. In addition, native Indians employ a variety of salmon catching methods in their food fisheries. Each type of gear requires a different fishing technique, and is subject to a different set of regulations. All, to a greater or lesser degree, harvest a mixture of species, stocks, broodlines, and life history types.

The gill net is the traditional river mouth gear, but gill nets are also deployed very effectively wherever fish are concentrated on the return migration, such as the narrow entrances to the Strait of Georgia and in channels between islands. Purse seiners also depend on concentrations of fish and are most effective near shore, adjacent to river mouths, or in the approaches to spawning streams. Commercial trollers fish by hook and line. Although they can capture maturing fish approaching the river mouths, trollers normally fish further seaward along the migrations routes and exploit immature as well as maturing fish in the oceanic feeding grounds. In British Columbia the sport fishery is mainly an inshore, sheltered water fishery. Currently the Strait of Georgia, being the sheltered water nearest the major population centers, supports most of the effort. As the sports fishermen become more mobile, with better boats and equipment, more remote areas of the coast are becoming accessible to them.

Traditionally there has been a kind of species separation among the gear types. In the past, gill-netters and purse seiners fished mainly for pink, chum, and sockeye, and these were considered to be the "net" species. Commercial trollers fished for coho and chinook. The sport fishery was considered a minor component of the system that also harvested coho and chinook. Currently, this traditional separation is breaking down. Trollers are learning how to catch the net species, and the high value of all species makes it profitable for seiners and gill-netters to pursue the rarer coho and chinook. The sport fishery is no longer a minor component, but harvests almost 350 000 chinook and 500 000 coho. These figures represent over 20% of the coastwide catch of chinook and 13% of the coastwide catch of coho (Argue et al. 1977). The combined fishing power of the sport and commercial fleet is so great that it is capable of fishing out most stocks within a single season. In some areas commercial fishing periods of 1 d/wk or less are required to prevent severe overexploitation of even the strong stocks.

The physical deployment of commercial gear types along salmon migration routes is such that the returning fish must find their way through successive concentrations of different types of gear to escape upstream to spawn. The term "gauntlet fisheries" describes this deployment of gear (Beverton and Holt 1957, Paulik and Greenough 1966). Such fisheries operate in the approaches to all major spawning rivers, and harvest a complex mixture of species and stocks. At the river mouths a terminal net fishery normally operates to take any surplus fish that escape through the gauntlet fisheries. Terminal fisheries exploit a smaller collection of stocks but nevertheless are still mixed stock fisheries. As examples I shall briefly describe the gauntlet fishery on pink salmon runs returning to

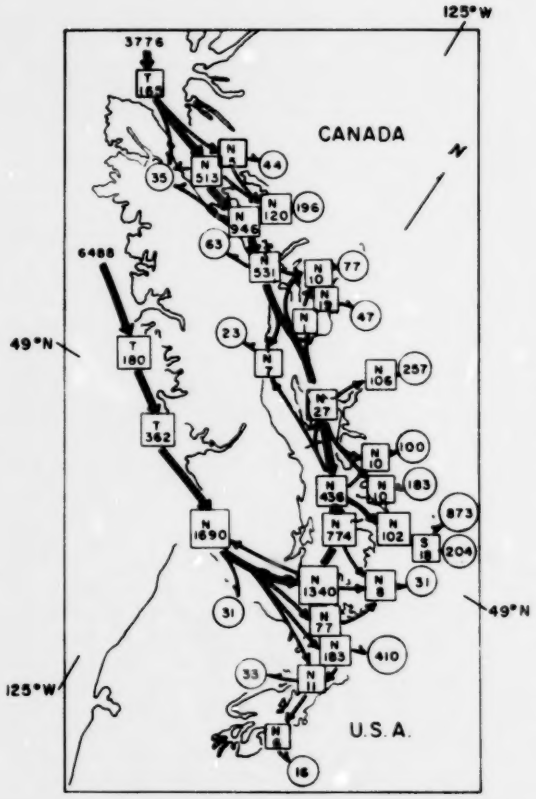

FIG. 4. Pink salmon runs to the Strait of Georgia and Puget Sound and the guantlet fisheries harvesting the runs. Squares represent fisheries, circles spawning escapements. T = troll fishery, N = net fishery. Number within a square or circle is the catch or escapement in thousands of fish. Adapted from Vernon et al. (1964) for the 1959 run.

the Strait of Georgia and Puget Sound, and the terminal fishery on all species at the Fraser River mouth.

In odd years, about 8 million pink salmon approach the Strait of Georgia and Puget Sound through Johnstone and Juan de Fuca Straits. Most of these fish are bound for the Fraser River, but the run also includes fish bound for many other rivers (Fig. 4). On their way to their natal streams the pinks are exploited by troll, seine, and gill net fisheries all along their migration route (Fig. 4). This is the typical gauntlet fishery (Vernon et al. 1964).

The spiderwork of arrows in Fig. 4 represents the migration and exploitation of only one species returning to a small area of the coast. Furthermore, the arrows depict not individual stocks in all cases, but mixtures of stocks such as "early" and "late" Fraser River pinks, and "mid Vancouver Island" pinks. On top of this representation for pink salmon, similar representations for the other species that are harvested in the same waters at similar times of year could be superimposed. With this degree of complexity it is easy to imagine

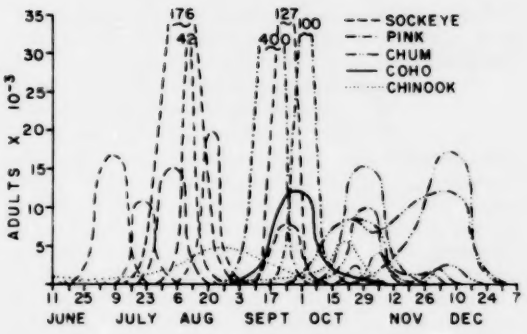

FIG. 5. Stocks and mixtures of stocks of the five species of Pacific salmon returning to the mouth of the Fraser River, and their relative abundance.

the frustration of attempting to manage the gauntlet fisheries on a stock by stock basis.

Even in terminal fisheries at the mouths of the larger rivers, such as the Fraser River, a dismaying conglomeration of overlapping runs of many stocks is harvested (Fig. 5). As with the pink salmon run in Fig. 4, the curves in Fig. 5 in many cases depict mixtures of stocks. A complete representation of the stocks would be even more complex. Terminal fisheries have the single advantage that the manager usually has to deal with only one gear type, the gill net. This advantage is of little consequence when, as often happens, a weak and declining stock so overlaps with a strong stock that no degree of nimbleness on the part of the manager will permit exploitation of the strong stock and protection of the weak stock. Apart from the loss of potential productivity, the disappearance of weak stocks in a mixed stock fishery is of concern because of the possibility that unique gene pools may also be lost.

Management to protect weak stocks is not the only priority of the fishery manager. Allocation among gear types in the gauntlet fisheries is a significant problem for which there is no established policy guideline. Allocation among user groups is an equally controversial issue. The principal users are commercial fishermen, recreational fishermen, and native Indian subsistence fishermen. Each of these groups stridently demands a greater share of the dwindling resource, and all are politically active in pursuing their demands. In almost every instance the fishery manager is squeezed between the demands of both the gear types and user groups for more of a share in the catch and the need to let more salmon through the fishery to the spawning grounds.

Superimposed on local management problems created by the multitude of species, stocks, gear types, and user groups are more general problems having to do with the number of political jurisdictions that have some vested interest in salmon. In British Columbia, the Federal Government is responsible for stock conservation and management of the salmon fisheries, but the Provincial Government has a significant stake in the fishery as well. Internationally Canada must deal with the United States, and, to a lesser degree, with Japan, in regulating the ocean fisheries for salmon. British Columbian fishermen catch salmon originating in Washington

and Oregon, whereas Alaskan fishermen catch salmon originating in British Columbia. Negotiations are under way to regulate the fisheries of both the United States and Canada to an equitable rate of interception. By international agreement, Japan does not fish east of 175°E, and presumably captures few British Columbia salmon as a result. Extension of the Japanese land-based fleet into more southerly waters, where they are catching a lot of sockeye and coho, however, has brought into question the adequacy of the present fishing boundary to protect British Columbia stocks.

If we consider the whole internalized fishery system, we have about 8 political jurisdictions, 3 principal user groups, 4 gear types, 5 species, 3150 stocks, 17 brood lines, and an uncertain number of life history types with which to be concerned (Table 1). The salmon fishery, of course, is not an independent unit, but is affected by other sectors of the fishing industry, particularly market demand for various products of salmon, and by the herring fishery. A host of nonfishery external influences also affects decisions about the salmon fishery, including such things as economic conditions in the forest industry and the real estate value of stream bank building lots. Decisions about the management of salmon stocks must not only be compatible with conservation and sustaining yield, but also with allocation among competing user groups, competing gear types, competing political jurisdictions, and competing industrial and domestic uses of salmon habitat. Meeting these external demands severely restricts the range of opportunities for the biological management of salmon.

Current Management Practice

The current approach to the management of salmon stocks is based on a few fundamental assumptions. One of these is that there is some stock–recruitment relationship of the Ricker (1954) or Beverton and Holt (1957) type, such that maximum yield occurs at a stock abundance below the equilibrium abundance in the absence of fishing. The management rule derived from this assumption is to regulate the fishery to permit optimum escapement. The quantitative application of stock–recruitment theory would provide two important predictions for the management of salmon fisheries. It would predict optimum spawning stock for greatest long-term yield. In the event that the actual spawning stock was greater or less than the optimum, it would predict recruitment from the spawning stock so that the fishery could subsequently be adjusted to bring escapement back to optimum. Unfortunately, empirical data collected over the years do not permit either prediction to be made accurately enough to override other pressures in management. Data on recruitment from a given stock are available for only a few mixtures of spawning populations, and these data are so variable that stock size for maximum yield is still highly uncertain (Fig. 6). Attempts to relate recruitment to some quantifiable life history stage closer to recruitment than the spawning population, such as fry or smolts, have also been unsuccessful in generating precise predictions of recruitment (Fig. 6).

Why the relationship between stock and recruitment is so weak is not clear. In part it may be due to errors in measurement of both stock and recruitment. The importance of variation in the ocean environment in regulating the numbers of salmon returning to spawn may also have been

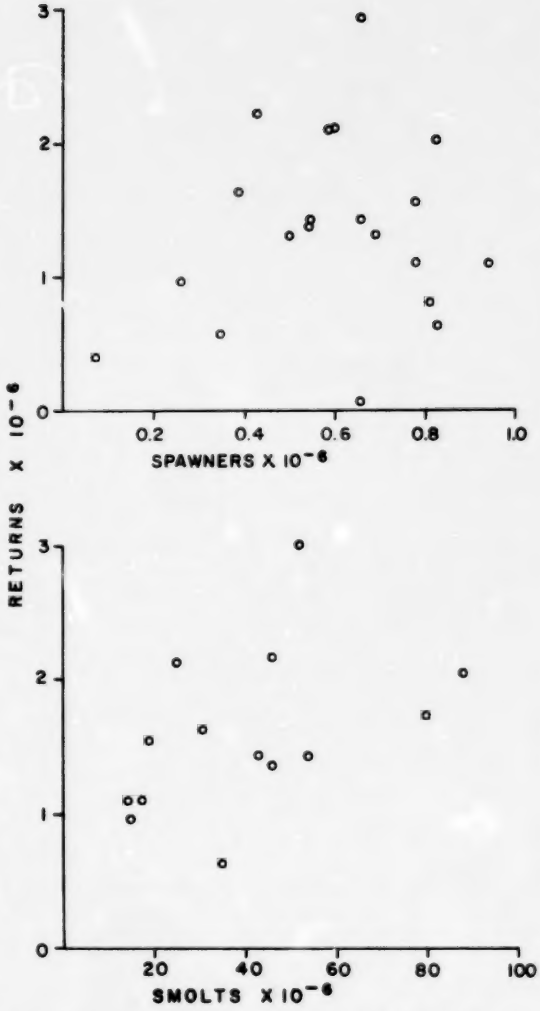

FIG. 6. Upper panel: stock and recruitment data for Babine sockeye salmon. Lower panel: the relationship between smolt production and adult returns for Babine sockeye salmon.

underestimated.

Imprecise predictions from a weak stock–recruitment relationship are not too serious in the case of single stock management, because adjustments can be made within the indicated range of sustainable yields to conserve the stock. Poor predictions are much more serious in the case of a multistock fishery where one objective is to protect unproductive stocks from overexploitation. Where many stocks are involved, the kind of juggling with exploitation that can be undertaken with a single stock is practically impossible.

A second fundamental assumption derived from stock–recruitment theory is that, in a mixed stock fishery, taking maximum long-term yield will result in the extinction of the weakest stocks (Paulik et al. 1967). Because most

Pacific salmon fisheries are mixed stock fisheries, and hundreds of stocks are often involved, one could conclude that salmon management biologists were in an ideal position to test the predictions of this theory. Unfortunately, we have not proceeded in this manner. The fisheries have not been viewed as experimental units. Even if they had, I doubt that completely satisfactory tests could have been devised. It is highly unlikely that the fisheries could have been manipulated with regard only for the testing of hypotheses, yet this would have been necessary to provide unequivocal results.

What has occurred is the severe depletion of some stocks. This observation has tended to confirm the theory in the minds of some. The argument is tautological, however, the prediction of the theory being that weak stocks will decline, and the conclusion being that those stocks that declined must have been weak. In the absence of good stock–recruitment relationships for the stocks involved there was no way to predict, a priori, which stocks would decline. Nor has the decline in some stocks provided us with the knowledge to predict future declines, or recoveries, as a result of changed regulations. In many instances we lack such basic information as the relative rates of exploitation on different stocks in a mixed stock fishery, or even the detailed stock composition of the fishery.

Lack of good population data is not the only impediment to interpreting declines in stock size. The fishery has not been the only factor contributing to declines in stock size, and it is always possible to find a number of plausible explanations for any change in abundance. Furthermore, high variability in recruitment rate, imprecisions in measurement of catch and escapement, and the fact that only a few stocks have been monitored for any length of time mitigate against relating changes in stock size to any specific cause.

Larkin (1979) has described the management of the salmon fishery as highly sophisticated. Despite this apparent sophistication, the practical management of salmon fisheries is very much a seat-of-the-pants operation. The behavior of stocks is highly uncertain. Imprecise preseason forecasts of stock size must be continually revised as each year's fishery develops. Policies respecting conservation and allocation of the catch are seldom explicit, and the individual manager must often decide trade-offs between declining stocks and the exploitation of strong stocks in gauntlet fisheries. Long-term goals and objectives for the fishery are, at best, unclear. The manager must juggle with these uncertainties in the midst of the fishery, when user groups are clamoring for a bigger share and a bigger total catch, and opening the fishery for an extra day can make the difference between an adequate escapement and severe overfishing for some stocks. It is a tribute to the skill and dedication of the managers that the whole fishery is not in chaos. A measure of their success is the fact that British Columbia's salmon stocks have declined less than United States or Asian stocks. The stocks have, nevertheless, declined, and it is important to ask whether the developing theory of multistock fisheries can be of assistance in managing the salmon fisheries, from the point of view of both stock conservation and of designing regulations for mixed-stock fisheries.

The Application of Mixed-stock Fishery Theory

With regard to stock conservation in multistock fisheries two determinations are critical. These are the order in which the stocks will be eliminated as exploitation rate is increased, and the rate of exploitation at which elimination will occur. The theory of mixed-stock fisheries should be of assistance in making these determinations. For a number of reasons, however, the current theory is inadequate to the task. First, the theory is based mainly on the Schaefer catch and effort model, or on the Ricker stock and recruitment model (e.g. Ricker 1958; Paulik et al. 1967; Pope 1976a, b; Horwood 1976; Hilborn 1976). Salmon catch and effort data do not fit the Schaefer model well, nor do salmon stock and recruitment data fit the Ricker model well. Second, the theory is currently developed for mixtures of two stocks, with the exception of Paulik et al. (1967) who considered a mixture of up to 20 stocks. Most salmon fisheries exploit at least 20 stocks spread among several species. Third, even if an appropriate model was found to describe salmon stock behavior under exploitation, its application would almost certainly involve measurements of relative exploitation rate and stock composition in multistock fisheries. The costs and uncertainties associated with monitoring individual stocks in the fishery would probably preclude practical application of such a model in all but the most desperate circumstances.

With regard to designing regulations for mixed-stock fisheries, current theory does provide useful insights. In particular, Pope's discussion of the effect of competition and predation in mixed fisheries (Pope 1976a) is useful in directing management decisions where competition and predation are suspected among stocks. As with stock–recruitment theory, however, the usefulness of mixed-stock fishery theory is mainly qualitative at present.

It is an unfortunate conclusion that the current theory of mixed-stock fisheries is of limited value in the practical management of multistock salmon fisheries. In my view, however, we need some assistance beyond the traditional fishery models in making decisions about salmon management. We need models that can cope with high uncertainty in parameter values, and that can take account of potential economic and social consequences of management decisions that may result in changes in stock abundance. Techniques developed in engineering, industry, and economics to deal with complex problems involving high uncertainty, such as control theory, stochastic dynamic programing, and utility functions, appear to have promising application in fisheries management (Walters and Hilborn 1976; Keeney 1977; Hilborn and Walters 1977; Walters 1975, 1977). These techniques have not yet been used to deal explicitly with problems of multistock fisheries, with the exception of Hilborn's (1976) discussion of the application of stochastic dynamic programing to a two-stock fishery. Multistock fisheries are, nevertheless, of the class of problems to which these techniques apply. Their attractiveness lies in the fact that they provide objective ways to evaluate alternative management strategies and to determine fruitful experiments to improve predictability (Walters and Hilborn 1976).

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Ecological Approaches to Stressed Multispecies Fisheries Resources

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The importance of a multispecies approach to management of freshwater fisheries is demonstrated by the history of fisheries in the Great Lakes and elsewhere for which comparable analytical and/or historical records are available. Moreover, findings from our empirical, comparative modeling approach to study small ecosystems demonstrate the overriding importance of the morphological and limnological variables in determining the structure of fish and planktonic communities. The effect of man-made stresses on the biotic community often seems to be mediated through their effects on abiotic factors. Fishing intensity, extant species assemblages, and environmental factors all seem about equally important in determining the yield characteristics and appropriateness of different, protective regulations.

Key words: multispecies, management, empirical modeling, effect of morphology, effect of limnology, yield, protective regulations, man-made stresses

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L'historique des pêcheries des Grands lacs et autres régions pour lesquelles des données analytiques et (ou) historiques comparables sont disponibles démontre bien l'importance d'une approche multispécifique de la gestion des pêches en eau douce. En outre, les données obtenues par notre modélisation empirique comparative dans l'étude de petits écosystèmes démontrent l'importance primordiale des variables morphologiques et limnologiques dans la détermination de la structure des communautés ichtyologiques et planctoniques. L'effet des contraintes imposées par l'homme sur la communauté biotique semble se produire par l'intermédiaire de leurs effets sur les facteurs abiotiques. Quand il s'agit de déterminer les caractéristiques de rendement et la pertinence de diverses réglementations de protection, l'intensité de la pêche, les groupements d'espèces actuels et les facteurs ambiants semblent tous revêtir à peu près la même importance.

Introduction

During the past 5 decades "multispecies approaches" have been applied in many practical situations, sometimes with assistance from scientific researchers. Some of these recent approaches may owe something to the rural traditions (craft, guild, or trade) that have thrived in continental Europe with respect to small fisheries and fish culture during the past 5 centuries. But little of what has happened in the West owes much to the Chinese folk wisdom on such matters that began to accumulate perhaps as long as 5 millenia ago (Tapiador et al. 1977).

Though it is obvious that many experts know a great deal about particular multispecies fisheries or similar sets of such fisheries, there exists no general compendium on the subject. Bits and pieces of an historical literature are now emerging; perhaps it will soon be appropriate to assemble a first compendium.

There is still that common, though mistaken, presumption that only those approaches first developed for marine fisheries are likely to prove useful there. A difficult substantive problem relates to the differences in *scale* between the multispecies fisheries of the Grand Banks and those of smaller inshore areas or of freshwaters. With respect to area involved and biomass of the harvest, the Grand Banks case dwarfs all those in which current multispecies approaches are being applied to good effect. (But the Grand Banks case is still comparatively simple with respect to human usage of the whole ecosystem; more about this later.)

In practice, how do fisheries researchers transfer ideas and techniques from small ecosystems to large ecosystems and vice versa? It has been done, most notably by R. M. Jenkins and his colleagues on at least three different occasions. Jenkins was trained in the 1940s in the use of experimental designs and statistical techniques that R. A. Fisher and G. W. Snedecor were developing for agriculture, broadly defined. He used limnological ideas and generalizations, e.g. those developed by D. S. Rawson for some medium-sized Canadian lakes, first with respect to small Oklahoma farm ponds and then to sizable reservoirs in the southeastern USA. Jenkins and colleagues soon applied some predator–prey concepts developed by H. S. Swingle for farm ponds to large reservoirs (Jenkins 1957, 1977). Meanwhile, H. S. Swingle and his colleagues extended their ideas to small lakes. One of the techniques that was developed to assist in the application and extension of Swingle's approaches to American reservoirs was "cove rotenone sampling"; several symposia have been convened on this subject (for references see FAO 1978, 1980).

Rawson's limnological initiative was developed, in a somewhat different direction from that of Jenkins, by R. A. Ryder and colleagues (Ryder et al. 1974). It was extended to other sets of lakes and reservoirs in various parts of the world, including some quite large waters and some that are

quite small (Welcomme and Henderson 1976; Welcomme 1979a, b). By now at least a score of limnological variables have been demonstrated to be correlated to some extent with fish harvests in multispecies situations, sometimes with sufficient accuracy to serve predictive or forecasting purposes (FAO 1978, 1980). For example, Jenkins has found the following variables to be most important for his reservoirs: water area, reservoir age, mean and maximum depth, water level fluctuation, outlet depth, thermocline depth, length of growing season, total dissolved solids (excluding chlorides and sulfates where these are excessive), shore development, and water exchange rate.

The two examples cited above do not exhaust the list of approaches that have been extended from ecosystems of one scale of magnitude to ecosystems of a very different scale, or that have been extended from one type of ecosystem (lake) to different types (ponds, reservoirs). However, as far as we know, no comprehensive review of experience with such transfers exists. On the basis of past experience, could R. M. Jenkins now provide sound advice on how the various techniques, currently being used by him and his colleagues, might be applied with Grand Banks fisheries? If so, what would be the underlying model and presuppositions that he would use? From recent discussions with him, we judge that he would take a comparative empirical approach and would expect to find the following variables to be important: standing stock of nutrients and exchange rate of nutrients in the euphotic zone, water depth, growing season, and the predator–prey balance in the fish association.

A first attempt to expose the role of the scale aspect, as it might influence the selection of particular models and methods for a particular fisheries problem in a particular ecosystem, led one of us to propose a three-dimensional formalism. For three variations on that theme see Regier and McCracken (1975, fig. 7), Regier (1977, fig. 16), and Regier 1978, fig. 6.1); space does not permit a reiteration here.

An attempt to explicate further some aspects of the formalism identified above led to the development of Table 1. It illustrates one way of classifying the multitude of approaches that have been used in fisheries. Implicitly it also explains the rather low precision that is characteristic of much of the past management-related information derived from research. One of the main points that we will emphasize in the next section is that the low precision is not all due to the unpredictability of fish populations but is due in part to the failure to consider appropriate environmental covariates that perhaps could explain much of what now appears to be random noise in different multispecies fisheries.

Experience with Modeling

A traditional approach to marine fisheries biology, i.e. to study each of the major commercial species almost in isolation, was needed to establish the basic parameters of each exploited species. The philosophy behind such an approach has now been largely abandoned, at least in theory if not always in practice. The multilevel integrated nature of an ecosystem is now well established although, apart from small isolated laboratory or field systems, the linkages between the parts of the systems pose a major sampling and methodological problem. As Platt and Mann (1981) point out, even when whole marine or freshwater ecosystems have been studied, the emphasis has been to establish the biomass levels of species or species groups while the fluxes between the different groups have been largely left to be inferred from species or group characteristics. This is in direct contrast with the practice followed in modeling the productivity of an ecosystem.

In any systems analysis type of model normally simulated on a computer, the linkages, the magnitude of fluxes, and the dependence of the fluxes on recipient and donor compart-

TABLE 1. Some interrelationships between ecological, mathematical, and practical features of fish resource management.

Important ecological variables	Type of mathematical approach	Realistic management goal	Basic management philosophy	Specialization of resource use	Example fisheries, dates	Relevant scientific studies
Fixed, or 50-yr cycles	Deterministic optimization	Optimum econ. yield	Purposive, explicit goal	Complete, with vert. integr.	NE Pacific halibut, 1940	Economists, W. F. Thompson
Gradual cycles, 25-yr period	Probabilistic, max. likelihood	Maximum sust.yield	Normative, approx. goal	Some hedging, balanced risks	North Sea plaice, 1950	Beverton and Holt (1957)
Frequent cycles, some surprises	Stochastic simulation	Optional sust. yield	Indicative, general goal	Mixed, balanced resource use	NW Atlantic pelagics, 1970	ICNAF
Some cycling, many surprises	Forecasting by extrapolation	Optional yield	Reactive, no real goal	Periodic flips, flexibility	Great Lakes, 1955–present	Loftus and Regier (1972)
No trends, only surprises	Real-time monitoring	Optional anything	Opportunistic, minimax	Almost no specialization	Kafue Flood Plain	Welcomme, Kapetsky

To begin understanding this table, presuppose a set of fish resource systems: (a) a resource system may be a single species of large biomass or an interacting set of species totaling a large biomass; (b) each system has moderate to large annual yield, 10^7–10^{10} kg/yr; (c) different members of the set exhibit a range of stability from fully predictable to utterly unpredictable; and (d) the harvesters of each fish resource system have adopted strategies and tactics relevant to the uncontrolled natural features of the resource system harvested. Also presuppose that the socioeconomic system is well behaved, i.e. "stable." If it is not, the practical applicability of the methods specified in the upper levels of the table diminish roughly in proportion to the degree of socioeconomic instability, and the applicability of the lower levels increases proportionately.

ments take on an overriding importance. Apart from the biomass values used to initiate the simulation, the biomass values become derived or computed parameters. The determinants of the flow between various compartments emerge as the invariants of the system.

The mathematical representation of the behavior of the ecosystem has taken many forms. Perhaps the most common approach has been to compartmentalize the ecosystem into a small number of fairly large units and elevate the process models that describe, for example, predator–prey relationships observed between two interacting species to describe the linkages between the aggregated compartments. This practice makes sense provided, of course, that the assemblages behave as if they were some kind of super species, an assumption that has not really been verified.

The second approach has been simply to assume linear and donor controlled flows between compartments (Patten 1971, 1972). Although this has been a fairly common solution to problems posed by the behavior of multicoupled nonlinear systems, one has the feeling that it is done for mathematical and computational simplicity rather than for any inherently ecological reason.

The third approach has been more holistic in its spirit. Here we include the search for ecosystem characterization by use of information theory, by its size spectrum, or by measures borrowed from statistical mechanics.

In viewing the present development, one is struck by the divergence of the different approaches. On the one hand there is the basic reductionist approach of compartmental flow models that, from one point of view, can be extremely complicated in terms of the number of compartments and linkages, and, yet, from another point of view quite simplistic in the sense that a few basic process models, differing only in parameter values, are used over and over again to represent the functional form of the linkages. On the other extreme we have the very general models or representations that measure some aspect of the coupling or the complexity of the system while ignoring both the biotic and the abiotic variables driving the system.

No doubt the reductionist approach appears more realistic. However, if it is the only way to proceed, it is questionable whether we will ever have enough information to model a lake or marine ecosystem well enough to answer such "simple" questions as to what is the economically or biologically optimal harvesting strategy of multispecies fishery? The only hope appears to be in the ability to find some abiotic and ecological master variables that govern the behavior of the whole system.

In reviewing what is generally known about the isolated parts of the ecosystem either from the laboratory, small scale field, or from theoretical studies, a few general principles emerge.

In the first instance we observe that both at the individual and population level the productivity per unit of energy or food consumed is maximum at some intermediate level. Hence, moderate predation tends to enhance the productivity of the prey species. In addition, predation may increase the number of coexisting, otherwise less competitive, species. Thus, total production may be enhanced due to exploitation of a wider spectrum of resources by prey of the exploited species (Regier et al. 1979, p. 339). The only practical alternative to detailed studies at the species level to decide the contribution of each species or species group to the productivity, and, ultimately, to the harvestable biomass may be through comparative studies of ecosystems differing in the structure of their biota; this is the approach adopted by the Lake Ecosystem Working Group (see Empirical Modeling).

Both normal predation and competition tend to dampen out fluctuations in species abundance. When this natural dampening is interfered with by overexploitation, violent fluctuations in the abundance of some species in the ecosystem are often observed prior to the collapse of the fishery.

Many single species studies have not brought out any demonstrable evidence to indicate that resources are limited to the extent that individual growth and/or recruitment are depressed. Such systems may be termed "predation dominant." On the other hand, low predation intensity (due to overfishing) can depress the productivity of prey species by increasing the competition among them to the point where much of the energy is going into maintenance. Many larger lakes appear to fall into this category. Smaller lakes or lakes heavily exploited for the resident piscivores tend to be "competition dominant." Both the growth and/or the recruitment are limited by competition for resources with an unreasonable fraction of available energy going into maintenance activities (Regier et al. 1979). The predation or competition dominance need not be a whole system characteristic but may, in any particular water body, change with each trophic level.

Generally speaking, ecological transfer efficiencies (food chain efficiency) tend to be rather low favoring short food chains for maximum harvestable production. There is some evidence, however, that the total or virtual absence of top predators due to heavy exploitation or some other externally generated stress with concurrent shortening of food chains may not bring about the expected increase in total harvest (Kerr and Martin 1970), perhaps due to the shift of the system from a predation dominant to a competition dominant state. At any rate, the level of productivity of an ecosystem, or any part of it, is not only a function of available nutrients and abiotic factors but also a function of its own biotic structure.

If we knew the existing and potential interactions in a multispecies system, we might be in a better position to design multispecies exploitation strategies to bring about a species and community structure that would result in an optimal harvest.

Research on single species populations points toward some unifying biotic regularities (K-line, P/B ratios) that appear to simplify the problem (Paloheimo and Plowright 1979). No such biotic regularities are as yet evident at multispecies or at whole ecosystem levels. (Powerful relationships between yield and abiotic variables have been recognized for decades in freshwater systems, see above.) However, our contention is that biologically meaningful statistics are almost totally lacking at multispecies or ecosystem levels for empirical observation of potential regularities or system invariants.

Empirical Modeling

Realizing that a modeling approach to multispecies fisheries problems was somewhat premature, we joined together, in 1976, with other colleagues in a group research study, i.e. the Lake Ecosystem Working Group (LEWG), that is

seeking to describe quantitatively how small lake ecosystems work and how they respond to acid precipitation, nutrient loading, and opportunistic fishing. LEWG is being led by J. E. Paloheimo and W. G. Sprules. Somewhat complementary to LEWG is a large Ontario lake survey project with respect to acid effects on fish associations (H. H. Harvey and A. P. Zimmerman) and a study on strategies and tactics appropriate for rehabilitating the Great Lakes (H. A. Regier). R. Knoechel, M. A. Gates, and B. J. Shuter are also active in LEWG.

A search for empirical generalizations governing the behavior of productivity in freshwater systems prompted LEWG to embark on a comparative lake ecosystem study by sampling a diverse set of lake types. The limnological and biological variables (phytoplankton, zooplankton, benthos, and fish) are sampled seven to eight times during the ice-free period. Contrary to our earlier statement of preference, only biomass levels of the size-related functional groups of species rather than fluxes between them are measured. The primary objective is to establish a few typical ecosystem structures that are explicable partly in terms of the morphological and limnological lake characteristics and partly by their internal species-group dynamics. Preliminary clustering of the planktonic communities shows four major lake types depending on the relative dominance of the edible phytoplankton, nonedible phytoplankton, herbivorous zooplankton, or carnivorous zooplankton. Much of what we have to say here will be documented in a forthcoming paper by J. E. Paloheimo, M. A. Gates, and A. P. Zimmerman.

In Table 2 we have listed the variables measured by the LEWG group on a diverse set of 29 lakes (1978). Canonical correlation analysis (cf. Cooley and Lohnes 1971) has been carried out to determine the overlap and redundancy between the various data sets, i.e. between the limnological (including morphological) variables, plankton, carnivorous and herbivorous zooplankton and fishes. For reasons not obvious as yet, the redundancy analysis failed whenever fish were included. Therefore, we have also calculated a more robust measure of similarity between the different data sets based on a Frobenius norm of intercorrelation matrix (cf. Lefkovitch 1976). The resultant similarities have been scaled so that unity indicates maximum similarity, and zero a complete lack of similarity.

If we consider only the phytoplankton abundance, 41% of the variability between the lakes can be explained given the limnology and lake morphology. However, when we include the effect of zooplankton grazing on the phytoplankton, i.e. calculate the redundancy in the phytoplankton data given the limnology and the herbivorous zooplankton, the variability explained goes up to 75%.

Inclusion of fish in the redundancy analysis invariably leads to numerical failure due to singularity conditions met in the matrix inversion. Although further studies may allow us to get around it, we have, meanwhile, calculated a measure of similarity between the various data sets (Table 2). The similarity between the total plankton and limnology is 0.50, between plankton, limnology, and fish, 0.56, and between limnology, fish, and plankton, about 0.61.

The emergence of significant redundancies and similarities among biotic and abiotic factors and among different ecosystem components gives us at least some hope that some regularities exist at the whole ecosystem level and that rational multispecies management through manipulation of

TABLE 2. List of variables measured in a survey of 29 small Ontario lakes (part A) and results of the redundancy and similarity analyses between different data sets.

A) List of variables measured.

		Plankton		
Limnology and morphology		Phytoplankton	Zooplankton	Fish
Secchi disk	Mean depth	5 spherical size-classes	5 herbivorous size-classes	31 species relative abundancies
Avg. temperature	Max. depth	2 filamentous size-classes	5 carnivorous size-classes	
Conductivity	Area	Numbers and biomass in epilimnion	Numbers and biomass in total water column	
pH	Volume			
Orthophosphate	Perimeter			
Dissolved O_2	% Littoral flushing			

B) Results of redundancy and similarity analyses based on seasonal average.

	Redundancy[a]	Similarity[b]
Phytoplankton given limnology	0.41 (0.33)	0.48
Phytoplankton given limnology + herb. zooplankton	0.75 (0.28)	0.52
Plankton given limnology	0.35 (0.42)	0.50
Plankton versus limnology + fish		0.61
Fish versus plankton		0.46

[a]Fraction of the variability explained by significant canonical variates. The numbers given in parentheses indicate redundancy in the second data set given sizes of the first one.
[b]Similarity based on Frobenian norm. The measure, unlike the redundancy, is symmetrical.

the ecosystem structure by regulated exploitation may indeed be possible.

Empiricism with Great Lakes Fisheries

The comparative approaches to fisheries developed by D. S. Rawson, H. S. Swingle, and numerous other workers was given another dimension in the SCOL Symposium (Loftus and Regier 1972). About a score of lakes that were taken to be natural replicates of each other within a functional limnological context were separated into different sets according to the nature of the particular man-generated stresses that had impacted each. The "sampling design" was analogous to that of a "randomized block design with unequal subclass numbers" in experimental agricultural work. Through a process of comparing and contrasting data within and between sets, the SCOL collaborators sought out generalities in the nature of the responses of the salmonid species associations to different stresses.

The SCOL approach was used with variations with the 1976 PERCIS symposium (Colby and Wigmore 1977) and the SLIS symposium on sea lamprey (Smith 1980). It is true that theory-oriented discourses occurred at all these three symposia, but the main intent was to discover first-order generalizations from historic records, time series, case studies, and well-informed opinion. As yet, no one has attempted to assess, in a comprehensive way, what has been learned from this kind of raw empiricism.

The following impressions emerged rather early in the process (see Regier 1973). (a) The major stresses act synergistically on these ecosystems, on the whole. (b) They have altered the fish association from one dominated by large benthic forms to one characterized by small pelagic forms; thus, competition may dominate over predation as the main mode of self-regulation (see above). (c) With the above change comes an increased variability in year-to-year landings of particular species. (d) The shift from large benthic to small pelagic species was not accompanied by a great increase in total biomass of marketable fish stocks, perhaps because the resources available to benthic feeders are not generally accessible to pelagic fish. (e) Market value per unit biomass is generally much lower with small pelagic than with large benthic species, and harvesting and processing costs are higher. (f) Thus traditional labor-intensive fisheries tend to disappear, though highly mechanized, capital-intensive enterprises can persist.

The above generalizations came out of the SCOL experience. Generalizations about opportunistic fishing were developed further as a result of PERCIS (e.g. Spangler et al. 1977) and SLIS helped greatly to understand the impact of the nonnative sea lamprey. Meanwhile other groups were making rapid progress in other empirical studies on these and smaller waters, especially on eutrophication and pollution by toxic materials.

Much of this empirical work was recently applied to a study on Great Lakes Ecosystems Rehabilitation (GLER) sponsored by the Great Lakes Fishery Commission (Francis et al. 1980). Currently GLER is in a further phase of its work which relates to clarification of strategies and tactics (the first phase dealt with feasibility).

The basic approach of GLER may be termed stress–response (or force–adaption or factor–modification or impact–perturbation) at the level of the ecosystem. A taxonomy of some 18 classes of major man-generated stresses has been developed (Table 3). Each of these 18 stress factors has been characterized with respect to major responses of affected aquatic ecosystems, especially of the fish association. The GLER group then summarized what is known about rehabilitation techniques with respect to each stress and about the feasibility of rehabilitation from technical ("ecological engineering"), economic, and institutional perspectives.

TABLE 3. List of human stresses on Great Lakes ecosystems.

1)	Fishing and other harvesting of biota
2)	Introductions and invasions of exotic species
3)	Microcontaminants, toxic wastes, and biocides, from industry and agriculture
4)	Nutrients and eutrophication from sewage plants, agricultural and urban runoff
5)	Organic inputs and oxygen demand from sewers, canneries, etc.
6)	Sediment loading and turbidity, from agriculture, construction sites, and resuspension
7)	Stream modification, e.g. dams, channelization and logging, changes in land use
8)	Dredging and mineral, sand, gravel, and oil extraction
9)	Filling, shoreline structure, offshore structure
10)	Water level control for shipping, electric power production, wetland management, etc.
11)	Dyking and draining of wetlands
12)	Weather modification, mostly industrial
13)	Water diversions between the Great Lakes Basin and other basins
14)	Entrainment and impingement in water intake structures
15)	Thermal loading from cooling water, mostly in electric power plants
16)	Ice control for navigation
17)	Major degradative incidents or catastrophes
18)	Acids and toxic chemicals transported by the atmosphere

The GLER group also characterized the present status of the sciences of ecology, economics, and political science as they relate to the more comprehensive issues of Great Lakes rehabilitation. They then tested the more general (overviews) and more specific (stress-related) perspectives through devising rehabilitation plans for two bays that have each been strongly impacted by many human uses. To summarize, the GLER group judged that rehabilitation is feasible. The Great Lakes Fishery Commission has continued the funding to develop the concepts and methods further.

With respect to marine fisheries, we judge that the GLER approach would prove useful for comprehensive policy-related research related to smaller bays impacted by a number of different uses and disparate user groups. The Apex of the New York Bight might be a prime candidate. If and when the Grand Banks falls under the concerted joint attacks of oil drilling, seabed mining, offshore pollution, as well as several kinds of fisheries, a GLER-like approach might prove helpful as an alternative to more detailed modeling studies.

In stressing eclecticism and empiricism in the preceding pages, we do not wish to slight theoretical approaches. But we do wish to emphasize that unique highly theoretical approaches have their greatest relevance either when very little is known about a particular case or when very much is known about it. In between those two extremes lies the broad

domain in which eclecticism and empiricism deservedly reign supreme.

Summary

Three main points have emerged from our discussion.

1) In the past many of the management-related studies tended to be rather vague both in their explanation of what has happened and in predicting quantitatively or qualitatively what will happen in the future in response to expected regulations and environmental changes.

2) In freshwater systems that experience a multitude of man-made stresses a broad, but almost inevitable, pattern appears to prevail. As the stress level increases, the top predators and the large benthic feeders disappear with the concurrent emergence of small pelagic forms supporting the few remaining fisheries. In some cases nonnative pelagic predators can be successfully introduced to prey upon the small pelagic species.

3) The major determinants of the freshwater, and probably also of the saltwater ecosystem structure, are typically morphological and limnological variables.

Any attempts to explain changes in multispecies fisheries that ignore concomitant changes in abiotic variables appear to be futile. Similarly, any modeling of the freshwater or marine system without incorporating the role of environmental variables also seems doomed to fail. Finally, we wish to re-emphasize the desirability of intensifying and broadening the growing interest in comparative fisheries research and the related forms of experimental or adaptive management (Christie 1978; Welcomme 1979a; Saila and Roedel 1980; FAO 1980, etc.).

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Southern Gulf of St. Lawrence Cod: A Review of Multispecies Models and Management Advice

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In the early 1970s, management advice for Atlantic cod (*Gadus morhua*) in ICNAF Division 4Vn (Jan. – April) and 4T was based on cohort analysis. In June 1975, a detailed analytical model of cod stock dynamics was introduced that explicitly considered growth and survival from eggs to adults. This model was revised and developed from 1975 to 1978, and eventually included the influence of mackerel abundance on cod recruitment. We review scientific advice for 4Vn and 4T cod and its basis. Analysis of the recruitment and production of the stock outside the period used for parameter estimation suggests that maximum net biological production of the stock complex may be achieved at a higher biomass level than previously estimated. Empirically derived models incorporating species interactions may mislead fisheries management due to the presence of spurious correlations.

Key words: Atlantic cod, mathematical model, numerical analysis, abundance, biomass, stock assessment

DOUBLEDAY, W. G., AND T. D. BEACHAM. 1982. Southern Gulf of St. Lawrence cod: a review of multispecies models and management advice, p. 133–140. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

Au début des années 1970, la gestion de la morue franche (*Gadus morhua*) dans les divisions 4Vn (jan. – avril) et 4T de la CIPANO reposait sur des analyses de cohortes. En juin 1975, on introduisit un modèle analytique détaillé de la dynamique du stock de morues, dans lequel la croissance et la survie, depuis l'œuf jusqu'au stade adulte, étaient explicitement pris en compte. Ce modèle fut révisé et perfectionné de 1975 à 1978 pour inclure éventuellement l'influence de l'abondance du maquereau sur le recrutement de la morue. Nous passons en revue les recommandations scientifiques touchant la morue de 4Vn et 4T, ainsi que leur fondement. L'analyse du recrutement et de la production du stock hors de la période utilisée dans l'estimation des paramètres laisse supposer que la production biologique nette maximale du complexe de stocks pourrait être réalisée à un niveau de biomasse supérieur à celui antérieurement estimé. Des modèles empiriques incorporant des interactions entre espèces peuvent induire en erreur les gestionnaires des pêches à cause de la présence de fausses corrélations.

Introduction

This paper was prepared at the request of the Workshop Steering Committee to contribute to the objective "review research on species and fisheries interactions and its impact on advice to fishery managers, to date." The Committee considered that the case history of southern Gulf of St. Lawrence Atlantic cod (*Gadus morhua*) would provide the Workshop with useful information on the extent of the influence of multispecies models on management advice and on the readiness of such scientific data and models for practical use. The southern Gulf of St. Lawrence cod stock was the focus of egg and larval cruises for several years, and information on adult abundance and vital rates was available from the commercial fishery and research vessel surveys. The dynamics of this stock complex had also been modeled both in research documents leading to management advice and in the primary literature.

History of the Fishery

The cod stock complex in the southern Gulf of St. Lawrence migrates from its summer area of distribution in the Magdalen Shallows region (adjacent to Gaspé and northeastern New Brunswick) to overwinter in Sydney Bight. Thus, the stock is exploited in the Gulf from May to December and along the edge of the Laurentian Channel in ICNAF Division 4Vn from January to April (McCracken 1959; Martin and Jean 1964). This migration pattern causes some difficulties in assigning catches from Sydney Bight to the appropriate stock complex.

Paloheimo and Kohler (1968) reported that cod had been fished in ice-free months in the Gulf for more than a century. Although early catch statistics are unreliable, catches apparently increased gradually from about 20 000 t in the early 1930s to over 40 000 t in the late 1940s. During this period, most fishing was by hook and line. The first otter trawling in the Gulf began in 1947 and foreign otter trawlers began to fish in Sydney Bight in the early 1950s. Total landings in the 1950s varied from 25 000 to 115 000 t, with very high landings in the late 1950s coinciding with a massive decline in herring abundance that was due to disease (Sinderman 1958). Gillnetting began in the Gulf in the early 1960s. The catch varied from 41 000 to 78 000 t in the 1960s (Lett 1978a).

The mean length of sampled landed fish declined from 61 cm in 1949–51 to 46 cm in 1962–65 (Paloheimo and Kohler 1968). Ages 9 and older were much less abundant in catches of the 1960s and later than they were in 1950.

Quota management of this stock by ICNAF was introduced in 1974. The Standing Committee on Research and Statistics (STACRES) provided annual scientific advice for this stock from 1973 to 1976. Since 1977, the Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) has taken over the advisory role of STACRES for this stock. The history of advised catch, total allowable catch (TAC), and reported nominal catches is shown in the following table (all figures in kilotonnes).

Year	Advised catch	TAC	Catch	4T	4Vn
1973			49.6	25.8	23.8
1974	68	63(60)	47.2	28.6	18.6
1975	50	50	41.2	28.8	12.4
1976	45(30)[a]	45(30)	32.8	17.6	15.2
1977	0–30	15	22.2	19.6	2.6
1978	25	27(38)	37.8	25.4	12.4
1979	50	36(46)			

[a]Figures in parentheses are revised.

Advice for 1974 was to maintain the 1972 level of fishing. During the period of decline of the catches, the scientific advice did not limit catches but did discourage the deployment of additional fishing effort on the stock.

Basis of Scientific Advice

Paloheimo and Kohler (1968) analyzed the fishery from 1949 to 1965. They were unable to find a statistically significant relationship between fishing effort and fishing mortality. Halliday (1972) applied Pope's (1972) cohort analysis to estimated catches from 1960 to 1970. He obtained a significant correlation ($r = 0.72$) between catch per unit effort (CPUE) of Gloucester class otter trawlers and "available biomass" (nos. at age × wt. at age × recruitment factor at age).

An extension of Halliday's (1972) analysis led STACRES in 1973 to advise that the annual instantaneous fishing mortality rate, F, in 1971 was slightly below F_{max} (F maximizing the yield per recruit) and that catches were likely to decline in 1972 and 1973. F_{max} was not specifically estimated in the relevant documents from the meeting. R. G. Halliday (Fisheries and Oceans, Bedford Institute, Dartmouth, N.S., personal communication) indicated that STACRES was unwilling to carry out formal yield per recruit calculations in view of the observed trends in increasing growth rates. Such trends continued to interfere with the use of standard catch projections throughout the decade.

The cohort analysis approach of Halliday (1972) also formed the basis for STACRES advice for 1975. In 1970–72 F was estimated to have been 0.50 and to have declined to 0.40 in 1973. F_{max} was considered likely to lie between 0.40 and 0.50.

The same approach was applied by STACRES at the April 1975 Assessments Subcommittee Meeting for 1976. Cohort analysis and Canadian research vessel survey data indicated that F in 1970–74 ranged from 0.40 to 0.60. The 1968 year-class was estimated to be very strong, the 1969 very weak, the 1970 average, and the 1971 stronger than average. The research vessel surveys began in 1957, but were first brought to the attention of STACRES by Hare and Kohler (1974).

The June 1975 annual meeting of STACRES saw the first of a series of analyses by P. F. Lett and co-authors on the recruitment mechanism and dynamics of cod in ICNAF Division 4TVn. The first such paper (ICNAF Res. Doc. 75/10) explained research survey egg abundance estimates from 1965 to 1972 by a quadratic function of age 4+ cod biomass, temperature, and time. Larval catches were explained as a linear function of temperature and egg catch plus a power function of time. A direct, density-dependent relationship was found between larval abundance and estimated abundance of the same year-class at age 2 from research vessel surveys. This paper was substantially revised and published (Lett et al. 1975). The estimation of egg catches was based on the transformation of $\sqrt{(\log (\text{eggs} + 1))}$, with a quadratic temperature term and the addition of the 1973 observation. The direct relation between larval catches and recruitment was dropped in favor of an indirect, asymptotic relation between predicted larval abundance and observed year-class size from cohort analysis.

The analysis was further refined and presented at the Special ICNAF meeting at Montreal in September 1975 by Lett and Doubleday (1976). A strong density dependence of growth rates was put forward together with a detailed analysis of the implications of various management strategies.

Based on this model and indicators of the status of the stock, the Assessments Subcommittee of STACRES advised extreme caution in setting the TAC for 1977 and revised downwards the TAC for 1976. The Subcommittee observed that the cod spawning biomass ranged between 70 000 and 90 000 t in 1973–75; 150 000 t was considered a stock biomass (ages 3 and older) giving stable yields of 40 000–50 000 t whereas slightly higher, but more variable, yields could be obtained at a biomass of 90 000–100 000 t. A TAC of 45 000 t recommended by STACRES in April 1975 was expected to give a fishing mortality of $F = 0.6$ in 1976 and TACs of 25 000–30 000 t were considered preferable, due to projected rebuilding of the spawning stock.

The model of Lett et al. (1975) was revised by Lett et al. (1976). Egg catches were explained as a linear function of temperature times change in weight of the mature stock (production). The logarithmic relation between eggs and larvae of 1975 was replaced by a linear combination of egg abundance and eggs × temperature. For the first time, the influence of mackerel on cod recruitment was hypothesized and included in the estimation of a modified Beverton and Holt stock–recruitment curve. For projections, the 1975 and later year-classes were predicted from the model equations, whereas the 1972–73 year-classes were estimated from research vessel data. STACRES advice was based on this paper, and further calculation led to a recommended TAC of 0–30 000 t, depending on the anticipated degree of reduction of the catch of immature fish.

Lett (1977) introduced a number of new concepts to the analysis of this stock complex. Density-dependent growth in

the 1st yr of life was discussed. Egg production was explained as a product of numbers of mature cod times a power (1.22) of the average annual gain of weight of mature cod times a quadratic temperature effect. Larval abundance was explained by the iterative solution of a differential equation for larval numbers over time. Larval survival (logarithmic scale) to age 2 was explained as a linear function of mackerel biomass, cod biomass, and larval abundance. Based on the current form of the dynamic simulation model, the average 3+ stock level associated with fishing at 2/3 F_{MSY} was 120 000 t with estimated catch at $F_{.20}$ (undefined) of 37 000 t in 1978. Due to uncertainties in the estimates, the TAC recommended by CAFSAC was 25 000 t.

Lett (1978a, b) updated his analysis of the 4TVn cod stock. The biggest change over previous analyses was the use of interactions of age 3+ cod biomass with the square root of age 2+ mackerel biomass in explaining recruitment at age 3. The influences of changes in efficiency of the fishing fleet and the influence of allocation policies to components of the fishery (gill nets, longlines, otter trawls) were examined. Based on the research document and related analyses, CAFAC advised a TAC of 50 000 t for 1979 with a possible 5000 t adjustment, depending on the allocations adopted.

In 1979 a CAFSAC research document by Gray (1979) formed the basis for a CAFSAC-advised catch of 63 000 t in 1980, assuming $F_{0.1} = 0.2$ and the 1979 TAC of 36 000 t would be exactly taken. The analysis incorporated a cohort analysis using commercial fishery CPUE, a yield per recruit calculation, and a projection with recruitment estimated from research vessel surveys.

The Model of Lett (1978b)

Lett (1978b) presented a model for management of southern Gulf of St. Lawrence cod that was based on several empirically derived relationships. A brief summary of these relationships is in order. Lowercase symbols b_i represent empirical regression coefficients differing between equations. Cod growth (G) was described as

$$(1)\quad \log_e G = b_1 \log_e B + b_2 \log_e B \times \log_e W + b_3 \log_e W \times D + b_0$$

where B = biomass of cod, W = weight of cod (kg), and D = dummy regression variable which represents the effect of an epizootic in herring on cod growth.

Production of eggs was related to spawning stock size as

$$(2)\quad \log_e E/N = b_1 \log_e \underset{\sim}{W} + b_2 T + b_3 T^2 + b_0$$

where W = weighted growth of the mature stock and T = mean surface temperature on the cruise collecting the egg samples.

Larval mortality was described as

$$(3)\quad \frac{dN}{Ndt} = b_1 \log_e N + b_2 (\log_e N) \times T + b_0$$

where N = number of eggs and T = annual monthly maximum sea surface temperature.

Numbers of recruiting age 3 cod (N_3) were described by

$$(4)\quad N_3 = b_1 L \exp (b_2 C \times M^{0.5} + b_3 C \times M^{0.5} \times L + b_4 L \times C)$$

where C = 3+ cod biomass at time N_3 was spawned, L = predicted abundance of larvae 50 d after peak spawning, and M = age 2+ mackerel biomass.

Density-dependent ℓ_1 growth in cod was described by

$$(5)\quad \log_e \ell_1 = b_1 \log_e N_3 + b_2 N_3 \times D + b_3 D + b_4 \log_e N_3 \times \log_e T + b_0$$

where N_3 = number of age 3 cod for the same year-class, D = dummy variable which accounts for herring epizootic, and T = temperature at Grand Rivière on May 25.

These equations form the basis of the simulation model outlined by Lett (1978a, b).

As discussed below, due to correlations and autocorrelations in the "predicting" variables and the use of stepwise regressions to seek out a "best fit," nominal statistical significance levels of Lett (1978b) are optimistic. Nevertheless, coefficients of variables such as temperature ($t = 1.51$, $P > 0.10$) and temperature squared ($t = -1.55$, $P > 0.10$)

TABLE 1. Abundance of cod ($\times 10^{-3}$) derived from groundfish surveys and from cohort analyses by Gray (1979).

	Research cruises				Cohort analysis ages	
	1	2	3	4	3	4
1970	42	6 887	15 069	14 551	51 404	46 216
1971	118	1 148	12 508	15 132	76 013	42 063
1972	1 478	4 193	9 196	24 553	27 444	62 233
1973	146	9 511	18 806	8 727	48 249	21 075
1974	160	4 671	20 431	14 375	69 844	39 161
1975	806	10 983	8 263	12 506	65 617	56 071
1976	5 998	14 844	64 245	16 128	122 573	51 570
1977	1 089	20 481	29 976	25 203	160 454	100 051
1978	2 365	9 707	43 924	47 326	150 000	130 796

in equation (2) are not nominally significantly different from zero. This also applies to the term $\log_e(\log_e N) \times T$ of equation (3). Thus, the model described by these equations is an hypothesis advocated by the author and partly supported by observation, and as Lett acknowledged it does not represent a final scientific solution to these problems. It differs from simpler empirically based models like Ricker's (1954) stock and recruitment curves only in the degree of complexity and the wider examination of variables and functional form.

Groundfish Surveys

Stratified random groundfish surveys have been conducted in the southern Gulf of St. Lawrence since 1970. These surveys have generally proved useful in predicting subsequent recruitment to the cod population. For example, the number of age 2 cod derived from the research cruises was related to the number of age 3 cod estimated from commercial fishery data by cohort analyses (Gray 1979) ($r = 0.93$, $n = 8$, $P < 0.01$) (Table 1). The number of age 3 cod in 1978 as input to the cohort analysis was uncertain and was set at 150 million (D.F. Gray, Bedford Institute, Dartmouth, N.S., personal communication). The number of age 1 cod in research cruises was not strongly related to the number of age 3 cod from cohort analysis that were present 2 yr later ($r = 0.54$, $n = 7$, $P > 0.10$). This result suggests that year-class size is not yet determined by age or that the research cruises do not accurately sample age 1 cod. Estimates of cod abundance in the research cruises agreed with those derived by cohort analysis for age 3 ($r = 0.72$, $n = 9$, $P < 0.05$) and age 4 ($r = 0.93$, $n = 9$, $P < 0.01$).

Egg and Larval Surveys

Egg and larval surveys in the Gulf of St. Lawrence for various fish species were initiated in 1965 and continued annually through to 1975. During that period, there were 35 cruises spanning 297 d at sea with sampling occurring at 2343 stations. From these cruises, estimated abundance of eggs and larvae of several marine fish species was obtained. One use of these estimates is prediction of year-class strength, and these variables have been incorporated into equations predicting cod recruitment (Lett et al. 1975; Lett 1978a). However, estimates of cod egg and larval abundance may be quite variable. The coefficient of variation of cod egg abundance for a May 1972 cruise was 2.57, that of a June 1973 cruise was 1.83, and that of a May 1975 cruise was 1.80. Estimates of larval abundance were more variable, with the coefficient of variation for a May–June 1973 cruise 3.98, and with the coefficient being 5.28 and 3.56 for 1974 and 1975 August cruises, respectively. If there is a relationship between egg or larval abundance and subsequent recruitment, high variability in egg and larval abundance estimates make detecting it difficult.

Data derived from egg and larval surveys can have several uses. If fecundity for a particular species is known, the surveys can estimate spawning stock size, a useful approach if numbers at age from cohort analysis are uncertain. This approach was used for Atlantic mackerel by Lett (1978b). Egg and larval surveys also provide information on identification of spawning areas, duration and timing of spawning, and delineation of nursery areas. These data are necessary for evaluation of environmental impact assessments, and can be useful to evaluate hypotheses concerning regulation of recruitment. For example, one may hypothesize that larval drift has a significant impact on recruitment, and analysis of hydrographic conditions in spawning and nursery areas may make a specific larval drift hypothesis implausible.

Growth

We have examined the evidence for density dependence of growth rates, length at sexual maturity, and growth in the 1st yr for southern Gulf of St. Lawrence cod. In a re-analysis of lengths back calculated from a body length/otolith length relationship, no evidence of density-dependent 1st yr growth could be found when size-selective fishing mortality was considered (Beacham 1981). Available evidence suggests that median length at sexual maturity may not be simply related to cod biomass as median length at maturity has declined during both periods of decreasing and increasing cod biomass.

To examine whether instantaneous growth rates, as determined by the natural logarithm of the ratio of mean lengths of a cohort in successive years, were dependent upon population biomass, we determined growth rates of age 5–8 cod and biomass of age 3+ cod from 1958 to 1978. Biomass was determined by using weights at age from Lett (1978b), numbers at age during 1967–78 from Gray (1979), and numbers at age during 1958–66 from Lett 1978b). The mean growth rate of ages 5–8 was inversely related with population biomass ($r = -0.67$, $n = 20$, $P < 0.01$), in agreement with the results of Lett and Doubleday (1976).

Comparison of mean weights at age from the winter otter trawl fishery (Lett 1978b) with those of summer research vessel surveys indicates systematically higher and less variable weights at ages 3–6 from the commercial fishery. This is readily explainable by the selection of larger than average partially recruited 3- to 6-yr-old cod by the commercial gear. Thus, growth rates in the stock for ages 3–6 were underestimated by Lett (1978b).

Fisheries Scientific Inference

The southern Gulf of St. Lawrence is not a laboratory and the 4TVn cod stock is not subject to rigorous experimental design. First, natural variation occurs as time series; second, measurement of alternative explaining variables is often imprecise or indirect. Time series observations reduce the discriminating power of data between hypotheses due to a tendency of spurious correlations to arise by joint occurrence of trends. The series of egg catches, adjusted to May 20 (Lett et al. 1975, Appendix IV(A)), is a case in point. The tabulated values can be explained as

$$\text{eggs} = 10.37 - 0.85\,(\text{year}-1960)$$

with $R^2 = 0.75$ and a value of Student's t of 4.63 "significant" at the 1% level of probability. This problem of false correlation is partly addressed by insisting that any relationships be "biologically meaningful"; however, overestimation of the predicting or causal significance of relationships derived from such data can occur. In particular, the abiotic

minimum in RIVSUM (Sutcliffe et al. 1976) (i.e. the discharge of rivers into the Gulf of St. Lawrence) occurs at the same time as minimum cod production, and may well indicate an environmental cause of the low recruitment of the early 1960s.

Correlations exist between mature cod biomass and production (increase in weight of cod stock) and between cod biomass and mackerel biomass over an extended period. Correlations between "independent" variables in a regression lead to correlations between parameter estimates and inflation of variances. Willan and Watts (1978) discuss the implications of this effect, called multicollinearity, on parameter estimates and predictive capability when standard statistical model assumptions hold. The determinant of the correlation matrix of independent variables is a key indicator of the losses (resulting from multicollinearity) relative to the ideal which could be achieved if nature could be freely manipulated.

The sample size needed to provide equivalent confidence regions to the ideal is inversely proportional to the pth root of this determinant, where p is the number of predicting variables. The determinant is zero if two variables are perfectly correlated and is 1 when all correlations p are zero.

For the two variable case, the determinant is $1 - p^2$. The square root of this quantity is recommended by Willan and Watts (1978) as a measure of the loss of predictive capability. In the simplest case, a correlation of 0.866 between two predicting variables is equivalent to using an orthogonal design with half as many points. The relevant determinant for the three variables predicting recruitment (Lett 1977, p. 17) is 0.26, indicating that losses due to multicollinearity are equivalent to a 36% reduction of sample size.

For various reasons, including cost, key variables are not precisely measured or can only be inferred indirectly. The temperature at Entry Island is not the temperature encountered by cod eggs, although it may be a close proxy. Estimates of egg and larval abundance from surveys have standard errors of 100% or more of the mean. The estimation of mackerel abundance is the subject of continuing controversy, with a peak of disagreement at the November 1976 Special Meeting of ICNAF, where estimates of stock size and appropriate TAC varied by hundreds of thousands of tonnes. Lett (1978b) observed that his estimates of mackerel abundance in the Gulf of St. Lawrence, based on egg surveys, exceeded those of Anderson and Paciorkowski (1978) for the entire Northwest Atlantic. These measurement errors are an unpleasant fact of life which reduce the discriminating and predicting power of analyses.

Although Lett and co-authors were aware of the limitations of available data and applied sound common sense in advising management measures for the short-term, some of the methods used in their analyses exacerbate problems arising from the above three considerations. Many of the important relationships (e.g. estimation of recruitment of cod at age 3) were estimated by stepwise regression of variables representing a second-order response surface in the predicting variables. The formation of interaction terms greatly increased the problems of multicollinearity with correlation coefficients of up to 0.995 between variables. Although some variables were forced to appear in the resulting regression equations, others were selected by the computer to minimize the residual variation. Because of this, the particular interactions chosen could easily be artifacts. For example, it is hard to see why cod year-class size should decrease as the product of cod biomass and the square root of the mackerel biomass. The use of stepwise regression analysis is a sophisticated way of "looking for correlations." In the 1930s to 1950s, some papers by Carruthers et al. (e.g. 1938) found close correlations between certain functions of wind strength at the time of spawning and subsequent year-class strength for herring, cod, and hake. The method used was simpler than the approach used for Gulf of St. Lawrence cod, but has qualitative similarities to the use of "statistical interactions." Gulland (1953) indicated how correlations as good as those of Carruthers could be obtained from application of his methods to tables of random numbers. As pointed out below, relevant data series for this cod stock are autocorrelated time series giving the possibility of "explaining" events by coincident trends.

Participants in the analysis and modeling of this cod stock realized that the calculated statistical correlations did not demonstrate causality and Lett (1978b, p. 83) stated that the model can only be tested by the accumulation of new information. The above problems face anyone analyzing the dynamics of wild fish stocks and there are no simple solutions, although most investigators would be less inclined to the consideration of complex statistical interactions and the drawing of bold conclusions than has occurred in this case.

Dynamics and Production of the Cod Stock

Although inference on the mechanisms of population dynamics of the cod stock should, in our view, be tempered by the considerations mentioned above, some facts can be established retrospectively with reasonable certainty. Pope's (1972) cohort analysis enables the past composition of a heavily fished stock to be estimated with considerable accuracy. The method assumes a natural mortality rate and calculates year-class sizes at age needed to explain observed catches. Estimates, in recent years, are highly dependent on an assumed fishing mortality rate in the last year, but stock sizes in earlier years depend only on estimates of catches at age and the natural mortality rate. We have examined the implications of a recent cohort analysis by Gray (1979) by performing a sensitivity analysis and the calculation of gross production (recruited biomass at age 3 plus growth in biomass of cod aged 3 and older) and net production (gross production less loss in biomass due to natural mortality) using estimators and a computer program developed by Rivard (1980).

Sensitivity analysis, again using a program described by Rivard (1980), shows that the assumed fishing mortality rates for 1979 have little influence on estimated stock size at age prior to 1974. Year-class sizes for the 1971 year-class onwards were estimated by Grey (1979) using research vessel survey data which correlated well with cohort analysis estimates. Errors in sampling and aging have very little effect individually on estimates of stock size and recruitment, but can lead to biases and equilization of estimates of year-class strength. This applies to estimated recruitment in the early 1950s when sampling was poor. A 10% error in the assumed natural mortality rate translates into a 9–14% error in estimates of year-class sizes (age 3) up to 1963. Bearing these sensitivities in mind, it is interesting to examine the history of stocksize and production.

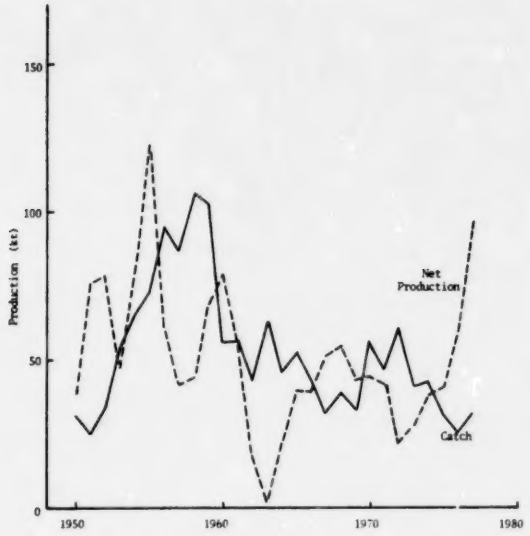

FIG. 1. Annual net production (recruiting biomass plus growth less natural mortality) and catches for southern Gulf of St. Lawrence cod.

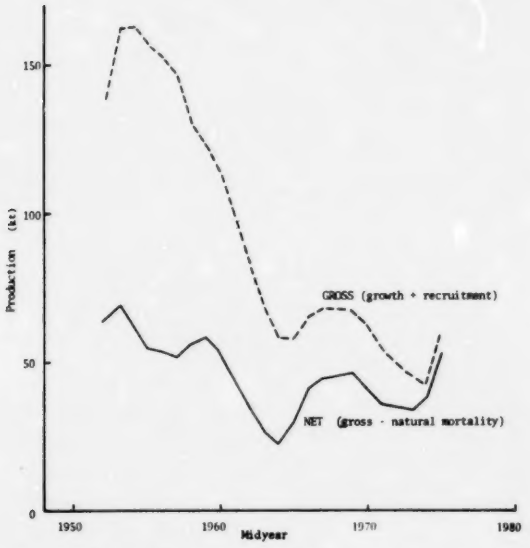

FIG. 2. Five-year moving averages of gross and net production.

The calculated annual net production of the stock and annual catches from 1950 to 1978 (Fig. 1) are biased due to the use of commercial fishery weights by age but are sufficiently accurate to show broad trends. Estimated net production varied from 1700 t in 1963 to 124 000 t in 1955. Catches followed trends in net production with about 4 yr delay. Although the estimated age 3+ midyear biomass varied from a peak of almost 500 000 t in 1956 to a minimum of about 90 000 t in 1974, net production was always positive. Thus,

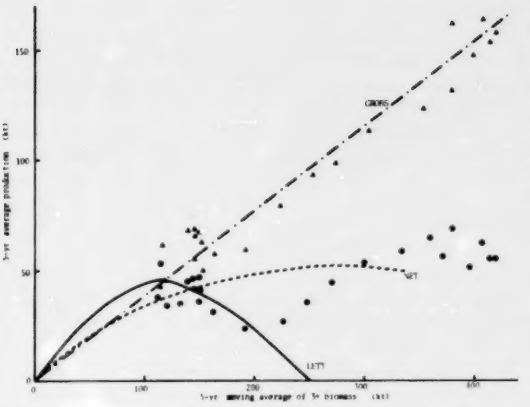

FIG. 3. Relationships between 5-yr moving averages of gross and net production, and biomass of age 3+ cod.

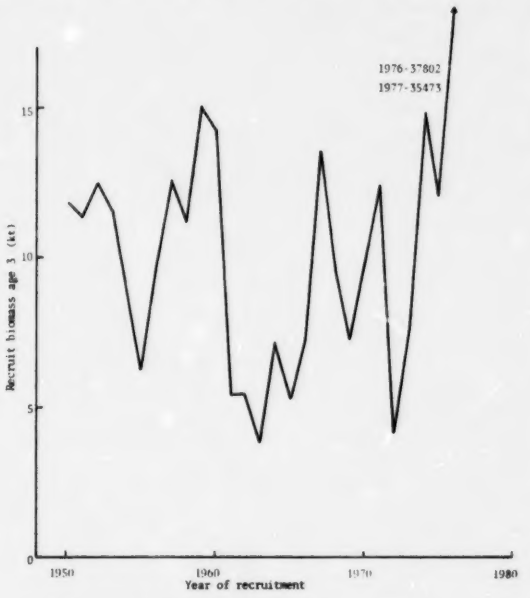

FIG. 4. Estimated annual recruiting biomass.

the decline in stock abundance was due to average catches exceeding average production for many years. Net production was higher at the biomasses of 300 000 t and over in the 1950s than at the biomass of about 150 000 t observed in the late 1960s. A declining trend in 5-yr moving averages of gross and net production is evident from the mid-1950s to the mid-1970s (Fig. 2). Deviations from the trends are partly due to series of strong or weak year-classes.

Gross production is very nearly proportional to biomass, whereas net production has a peak near 150 000 t with a decline near 200 000 t and another peak near 380 000 t (Fig. 3). The solid curve is approximately the cod yield curve of Lett (1978b) for the case of a mackerel biomass of

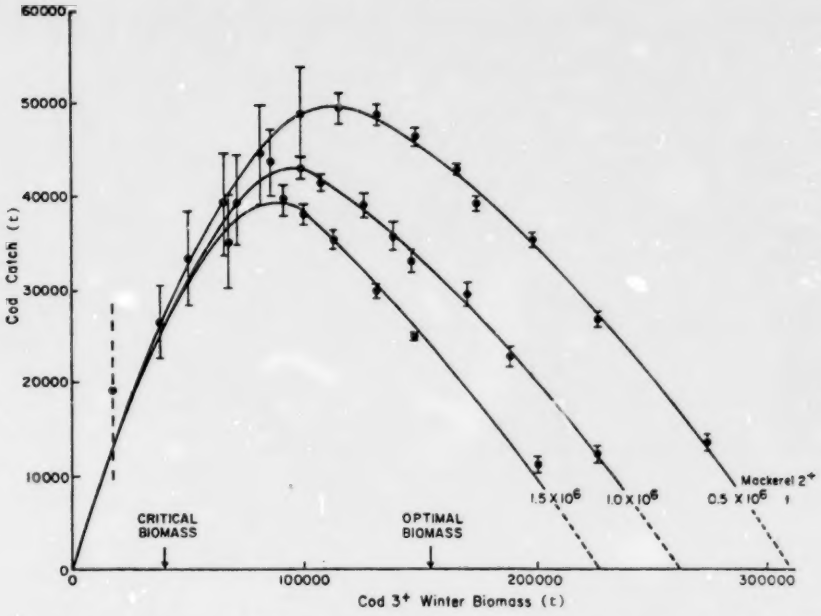

FIG. 5. Net yield versus biomass for southern Gulf of St. Lawrence cod (from Lett 1978b).

1000 000 t. The moving averages smooth year-to-year fluctuations and clarify trends. Plotting annual production (not shown) leads to similar results with much more scatter. The low net production observed in the early 1960s clearly departs from earlier and later patterns.

As the net production of the stock is largely composed of growth of age-groups 3–5 with recruiting biomass representing about 10% of gross production in most years, it is a series of two or three exceptional year-classes that cause high or low production. Figure 4 shows estimated recruiting biomasses at age 3 from1950 to 1975. The time series of year-class sizes is autocorrelated and, for numbers at age 3, there are estimated correlations of 0.554, 0.157, −0.253, and −0.277 for lags of 1–5 yr. High mackerel abundance has been invoked by Lett (1978b) to explain the weak 1969 year-class and a combination of cod and mackerel abundance to explain the poor recruitment around 1963.

Conclusions

Is equation (4) an accurate description of the recruitment mechanism of the 4TVn cod stock? The complex interactions of cod and mackerel abundance explain very well the events of 1954–72, leading to an hypothesis which can only be disproved outside this period. The historical average catches of over 30 000 t from the 1930s to the 1950s are very difficult to explain, assuming this relationship. Cohort analysis indicates that cod biomasses over 250 000 t gave good recruitment in the late 1940s and early 1950s. Research vessel surveys from 1975 to 1978 also indicate year-classes much greater than would arise from this relationship.

In view of these considerations, the confounding of trends in biotic and abiotic factors and the biological production relationships discussed above, we consider that density dependence is overestimated in this recruitment model. It is possible that very high mackerel abundance reduces cod year-class size, but it is likely that when mackerel are not extremely abundant, the maximum net production of the cod stock (50 000–60 000 t) occurs at 250 000 t or more and not at 120 000 t as implied by the above model.

What was the impact of the recruitment model, and particularly the species interaction, on management advice to date? Scientific advice on this stock became noticeably more definite in 1975 with the first detailed analysis. The model, which at the time of the September 1975 Special ICNAF Meeting had no mackerel component, strongly influenced STACRES in advising a middle course between conflicting views that cod stocks are very productive at low biomass levels (some European scientists) and that the fishery should be closed (some North American scientists). Recruitment projection by the model had very little direct effect on management advice as survey indices were available for ages 3 and older in the year of projected TACs. Estimates of density-dependent growth of cod, and of net production of various levels of cod and mackerel abundance, influenced the debate on allocation of quotas and the formation of a target biomass for the cod stock.

Lett (1978b, p. 111) shows the estimated influence of mackerel abundance on the net yield versus biomass curve of the cod stock (Fig. 5). Although changes in mackerel abundance by a factor of three induce a more than 25% change in cod yield, the "MSY" biomass is not changing substantially. Thus, mackerel abundance does not explain the high cod productivity of the 1950s. The model explains this high production using a "dummy" variable giving different cod growth rates. It is convincing to claim that some of the

increased growth was directly due to massive mortality of herring which was documented during this period, but this factor is unlikely to account for such an extended period of higher productivity. Mean lengths at age of cod in the NAFO Subdiv. 4Vn summer fishery and NAFO Div. 4W were also high in the 1950s. Better understanding of the causes of changed cod growth is needed before an optimal cod biomass can be confidently estimated. In view of the confounding of density-dependent growth of cod with possible abiotic indicators such as RIVSUM, an adaptive approach, monitoring vital rates and adjusting management policy annually, may be needed for many years to come.

The correctness of the optimal biomass estimate is crucial for the management of this cod fishery from 1979 onwards. Gray's (1979) analysis and 1979 research vessel catches indicate that the age 3+ cod biomass could be 400 000 t or more in 1980. Gillnet and longline fishermen tend to catch larger (hence older) fish than do trawlermen. If the stock is heavily exploited to reduce the biomass to 150 000 t there will be direct consequences on present and future allocations of catches as well as the long-term net production of the stock. Evidence to 1978 indicates that growth rates are declining, but recruitment may not follow suit.

The analysis of this and earlier papers on this cod stock has emphasized the effects of various factors on the cod stock. One observation can be made here, as has often been remarked about the North Sea cod: whether or not the net production of cod is highest at a stock size over 250 000 t, the gross production of cod, and hence the consumption of other animals by cod, increases more steeply than the net production and appears to be almost proportional to cod biomass. The negative effects of this consumption on other stocks have not been examined.

Data and analysis available in the mid-1970s led to a dynamic model which well explained what was known but had relatively little predictive capability. The target biomass for management arising from this model was not well estimated for reasons outlined above. It is not clear whether advice arising from the model was "better" than the yield per recruitment calculations which both preceded and followed it, the latter suffering from changing cod growth rates. Yield projections incorporating changes in cod growth rates would be a valuable aid in the management of this fishery.

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Cod–Capelin Interactions Off Northeast Newfoundland and Labrador

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AKENHEAD, S. A., J. CARSCADDEN, H. LEAR, G. R. LILLY, AND R. WELLS. 1982. Cod–capelin interactions off northeast Newfoundland and Labrador, p. 141–148. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

A review of seasonal distribution, fishery and population trends, and predation of Atlantic cod (*Gadus morhua*) on capelin (*Mallotus villosus*) is presented for the NAFO Div. 2J3KL cod stock and NAFO Div. 2J3K capelin stock. The effects of fluctuations in capelin biomass on cod growth and the inshore cod fishery were tested by correlation analysis. There were no statistically significant relationships between cod growth and cod biomass, capelin biomass, or water temperatures. The relationship between index of availability of cod to traps and one of the two available indices of mature capelin biomass was statistically significant. In addition there was a significant positive correlation between the total inshore cod fishery index of availability and one index of mature capelin biomass and water temperature. Because of uncertainties in the data, the relationships exhibited may not exist in nature and results from this study should be used only as basis for future research.

Key words: Atlantic cod, capelin, abundance, biomass, growth, population characteristics

AKENHEAD, S. A., J. CARSCADDEN, H. LEAR, G. R. LILLY, AND R. WELLS. 1982. Cod–capelin interactions off northeast Newfoundland and Labrador, p. 141–148. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

Les auteurs passent en revue la distribution saisonnière, les tendances de la pêche et des populations, et la prédation de la morue franche (*Gadus morhua*) sur le capelan (*Mallotus villosus*) pour le stock de morues des divisions 2J3KL et le stock de capelans des divisions 2J3K de l'OPANO. Une analyse de corrélation a servi à vérifier les effets des fluctuations de biomasse de capelan sur la croissance de la morue et sur la pêche côtière de cette dernière. Il n'y a pas de relations significatives à l'analyse statistique entre la croissance de la morue et sa biomasse, la biomasse de capelan ou les températures de l'eau. Par contre, la relation entre l'indice de disponibilité de la morue aux trappes et un de deux indices disponibles de biomasse de capelan mûr est significative. En outre, il y a corrélation positive entre l'indice total de disponibilité de la morue à la pêche côtière et un indice de biomasse de capelan mûr et température de l'eau. À cause des incertitudes des données, il se peut que les relations observées n'existent pas dans la nature. Les résultats de la présente étude ne devraient donc être utilisés que comme base de recherches futures.

Introduction

It is probable that cod (*Gadus morhua*) and capelin (*Mallotus villosus*) are the two most important fish species in the Northwest Atlantic, cod because of its position as the dominant commercial species (Pinhorn 1976) and capelin because of its importance as both a forage (Winters and Carscadden 1978; Bailey et al. 1977) and a commercial species (Anon. 1980). It is well documented that cod feed heavily on capelin both offshore (Turuk 1968; Minet and Perodou 1978) and inshore during the capelin spawning migration (Templeman 1965). However, apart from the feeding data little is known of the degree of dependence of cod on capelin although it has been speculated upon in the public media for years. For instance, even as early as 1835 fishermen were complaining that the "hauling of capelin for manure had proved very prejudicial to the success of the cod fishery" (Journal of the Newfoundland House of Assembly 1835).

The question of the impact of changes in abundance of capelin on cod dynamics and migrations might have remained unaddressed but for the initiation of an offshore capelin fishery in 1972. At that time, catches of ~71 000 t were reported in NAFO (formerly ICNAF) Subarea 2 and 3. Reported nominal catches rose rapidly and peaked at 360 000 t in 1976 and have declined since then. At about the same time, the Newfoundland–Labrador cod stock (2J3KL) had declined to its lowest levels. This combination of low abundance of a commercially important predator and a heavy fishery on a major food source accelerated both scientific and management interest in cod–capelin interactions and the extent of dependence of cod on capelin. Consequently, in conjunction with this Symposium on Multispecies Fisheries Management, the authors were asked to examine the available data in an effort to substantiate the cod–capelin interaction.

The purposes of this study were to review the distributions of both species and the patterns of cod predation on the capelin, and to investigate the effects of fluctuations of capelin biomass on the dynamics of cod, especially cod growth, and on the inshore cod fishery. The relationships between cod growth and cod biomass, capelin biomass, and water temperatures as well as the relationships between inshore catches of cod and cod biomass, capelin biomass, and water tempera-

[1]Authorship assigned alphabetically.

tures were investigated. To study these cod–capelin interactions in detail, stocks of both species from northeastern Newfoundland and Labrador were chosen. Although the stocks (Div. 2J3KL cod stock and Div. 2J3K capelin stock) do not occupy exactly the same geographical area, they are reasonably well-defined and do overlap to a large degree. In addition, cod predation on capelin is known to occur in this area and the data on the fishery and population dynamics for both species were generally better than for other areas.

Capelin Distribution

The distribution of juvenile and adult capelin (age 2 and older) is reasonably well-known (Jangaard 1974; Hinds 1975; Templeman 1948); however, there are gaps in our knowledge. Hence, the distribution maps (Fig. 1) reflect the known distribution of capelin; the absence of capelin from an area on the maps does not mean that capelin do not occur there. This discussion of capelin distribution encompasses more than just the Div. 2J3K capelin stock. Cod from the Div. 2J3KL stock probably feed to some degree on Div. 3L and Div. 3N0 capelin, two stocks that are believed to overwinter together on the northern Grand Banks. The time series of data for Div. 3L and Div. 3N0 capelin was not as complete as that of Div. 2J3K capelin and these data were not included in the following analysis; the more southerly stocks appear to parallel the 2J3K stock in annual fluctuations in year-class strength (Carscadden and Miller 1979). Their distributions are discussed here because of the probable relationship with Div. 2J3KL cod.

The major overwintering area for capelin appears to be northern Newfoundland for the Div. 2J3K stock and the northern Grand Bank for the Div. 3LN0 stocks; overwintering capelin also occur to a lesser extent on the southern Grand Banks, St. Pierre Bank, and some inshore bays in Newfoundland. It is not known whether capelin overwinter in Subarea 2. However, capelin do spawn in Labrador (Templeman 1948) and as there is no evidence for a northward migration from 3K, it seems probable that there are capelin overwintering in areas north of Div. 3K.

During March, capelin are beginning to form schools and move towards their spawning grounds. In Div. 3L, 3K, and probably 2J capelin move inshore during April and May while at the same time capelin from the Southeast Shoal stock are moving from Div. 3L to their spawning area in Div. 3N (Fig. 1).

By late May, most of the mature capelin are near the spawning grounds, either inshore or on the Southeast Shoal. Spawning begins on the beaches in late May or early June in southern Newfoundland and at about the same time on the Southeast Shoal. Spawning is progressively later further north; thus, spawning may not begin until late June or early July in northern Newfoundland and late July in Labrador. Capelin spawn on suitable beaches when water temperatures are 5.5–8.5°C although spawning has been reported in water temperatures as high as 10°C. When water temperatures exceed 10°C, the capelin spawn away from the beaches in colder, deeper water. Spawning continues for a period of ~4–6 wk in each area.

Postspawning mortality in capelin is very high and the few survivors (mostly females) move offshore in small scattered

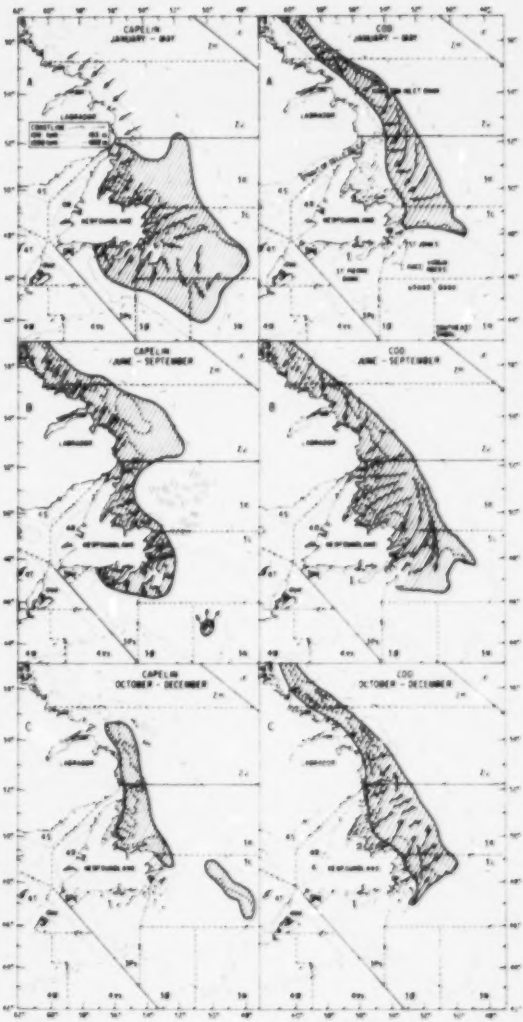

FIG. 1. General distribution of cod (Div. 2J3KL stock) and capelin (Div. 2J3K, 3L, 3N0, 3P stocks) for three periods of the year (A) January–May, (B) June–September, (C) October–December.

schools (Fig. 1). In early fall, these survivors and capelin maturing for the first time form feeding schools with the largest concentrations occurring in Div. 2J and 3K, where for a period of time in the mid-1970s there was a large commercial fishery. The pattern of the commercial capelin fleet suggests that there is a gradual southward movement from Div. 2J to the overwintering area in Div. 3K during October to December and that the major concentrations of capelin are within the 200-m isobath.

Capelin Fishery and Population Trends (NAFO Div. 2J3K)

Nominal catches of capelin reported to ICNAF by Canada

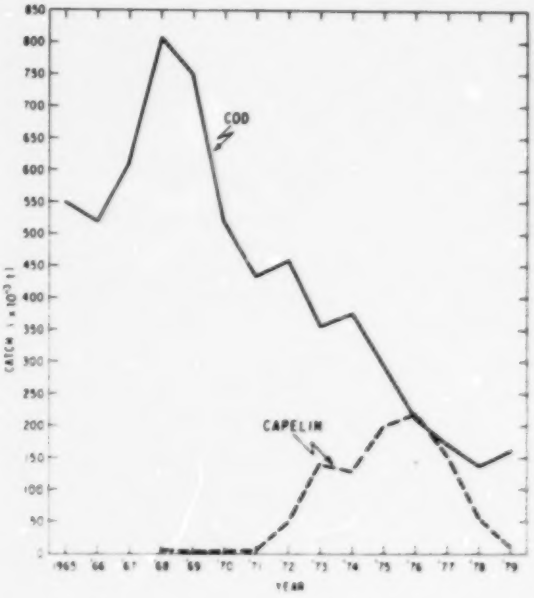

FIG. 2. Catches of Div. 2J3KL cod, 1965–79, and Div. 2J3K capelin, 1968–79.

for Div. 2J3K were less than 1500 t in the late 1960s and early 1970s. However, it is known that historically capelin were widely used on a domestic basis for food, fertilizer, and bait, and Templeman (1968) reported that total annual Newfoundland landings were once as high as 20 000–25 0000 t. An offshore fishery developed in Div. 2J3K in 1972 with reported catches of 46 000 t which rose to 216 000 t in 1976 and declined to 11 000 t in 1979 (Fig. 2). The offshore fishery was conducted by midwater trawls in September–December with peak catches usually in October and November.

There are two series of capelin biomass estimates available (Carscadden and Miller 1980; Carscadden and Winters 1980). The absolute biomass values differ quite markedly in the series; the patterns are similar in total biomass but there is no correlation between biomass estimates of mature capelin. In terms of total capelin biomass, one series (Carscadden and Miller 1980) shows a peak in 1976 of 7300 000 t and a decline to 780 000 t in 1979 (Table 1). The other series (Carscadden and Winters 1980) shows a peak in 1975 of 1300 000 t (although the 1976 biomass of 1250 000 t approaches this level) and a decline to 350 000 t in 1979 (Table 1). Although the differences in the capelin biomass estimates have not been resolved, both analyses indicate that fishing mortalities have been relatively low; hence it appears that poor recruitment in recent years has been the major cause of the decline in capelin biomass. Wide variations in capelin recruitment are not unusual. For example, recruitment in

TABLE 1. Annual growth increments of cod caught by the inshore trap fishery, NAFO Div. 2J3KL, and associated capelin biomass, cod biomass, and temperature, 1970–79.

	Cod growth increments (cm)				Capelin biomass[1] (kt)				Cod biomass[2] (kt)	July–June
					Mature		Total			
	2J	3K	3L	2J3KL	1	2	1	2	ages 4–7	TEMPSUM
Period	X_1	X_2	X_3	X_4	X_5	X_6	X_7	X_8	X_9	X_{10}
1970–71	—	7.4	4.6	6.0					1285	54.50
1971–72	5.0	3.1	5.8	4.6	1679	234	4261	720	1177	49.20
1972–73	6.7	4.0	5.9	5.5	2181	223	4581	837	900	4.29
1973–74	5.4	6.7	4.5	5.5	1978	254	4591	913	650	27.61
1974–75	9.2	9.0	7.5	8.6	1904	362	6123	1336	399	1.25
1975–76	5.5	6.8	5.9	6.1	2251	526	7310	1256	398	52.66
1976–77	10.9	5.8	7.6	8.1	3375	342	5641	781	751	42.92
1977–78	4.4	7.2	5.2	5.6	3405	218	3713	556	1006	39.13

Correlation matrix for periods 1971–72 to 1977–78

	X_1	X_2	X_3	X_4	X_5	X_6	X_7	X_8	X_9	X_{10}
X_1	0.24	0.89	0.89	0.24	0.26	0.41	0.30	−0.38	−0.30	
X_2		0.21	0.65	0.19	0.42	0.41	0.54	−0.74	−0.20	
X_3			0.84	0.17	0.38	0.50	0.37	−0.32	−0.20	
X_4				0.27	0.44	0.55	0.52	−0.64	−0.30	
X_5					−0.05	0.15	−0.49	0.15	0.29	
X_6						0.97	0.76	−0.79	0.29	
X_7							0.85	0.84	0.09	
X_8								−0.90	−0.29	

[1]Estimated biomass at January 1 of 2nd yr in cod growth period. Estimate 1 from Carscadden and Miller (1980); estimate 2 from Carscadden and Winters (1980).

[2]Estimated biomass at January 1 of 2nd yr in cod growth period. Calculated from Tables 7 and 10 of Wells and Bishop (1980).

Barents Sea capelin during 1951–61 fluctuated by a factor of 17 times (Gjosaeter 1972).

Cod Distribution

During January–May cod in Div. 2J3KL are concentrated mainly on the outer slopes of the Labrador and northeast Newfoundland shelf from Harrison Bank to the north cape of the Grand Bank (Templeman 1979) (Fig. 1). Spawning concentrations are in depths from 200 to 600 m and possibly deeper and in bottom water tempertures about 2.5–4°C. Off Labrador cod spawn mainly in March–April with most of the remainder spawning in May (Templeman 1964; Dias 1965, 1967). Some of the cod from northern Labrador, as far north as Div. 2GH, migrate southward during April–May to the southern Labrador coast and by June and July are appearing along the northeast coast of Newfoundland (Postolaky 1966). In general, however, during April and May the schools of cod are beginning to disperse and move over the tops of the banks and towards the coast.

The main coastward migration in June, when the cod of the Labrador–East Newfoundland stock move southward and westward toward the Labrador and Newfoundland coast, also coincides with the spawning migration of capelin to shallow water (Templeman 1979). These cod are homing to the general areas where they grew up as immature fish (Templeman 1979). During June–July, the 2J3KL cod stock is distributed from northern Labrador, southward along the Newfoundland coast in declining numbers as far as Cape Race and the Virgin Rocks, and as far westward as the entrance of the Strait of Belle Isle (Templeman 1974, 1979). It appears that the inshore migrations of cod are completed by August and the pattern of distribution is similar to that during June–July. Cod are also dispersed widely over the offshore and coastal banks during July and August. During September cod are still in the inshore areas of Labrador and eastern Newfoundland but there may possibly be some offshore movement.

The main offshore migration occurs during October based on evidence from tagging data which indicated that the tagged fish, migrating out from the coast, did not reach the offshore fishing grounds before October (Templeman 1979). By November–December the cod are beginning to congregate on the outer slopes of the continental shelf in the warmer deeper water where they remain and spawn during the winter and spring.

Cod Fishery and Population Trends (NAFO Div. 2J3KL)

Cod have been fished in Div. 2J3KL for hundreds of years mainly by vessels operating in coastal waters. Large numbers of cod migrate in the spring to shallow coastal waters where they are exploited by small vessels using a variety of gears including traps (= pound nets), gill nets, baited lines, and handlines. At this time capelin are spawning on or near the beaches and cod feed heavily on them. In the winter and early spring, large spawning concentrations of cod are fished by the otter trawl fleet particularly on the Hamilton Inlet and Belle Isle Banks. In the 1960s catches were unrestricted and were as high as 800 000 t but declined to 160 000 t in 1979 (Fig. 2). During the late 1960s and early 1970s, the cod population declined due mainly to an extensive fishery but also to a succession of poor (1969–72) year-classes (Wells and Bishop 1980). The biomass of cod of ages 4–13 in 1976 was about 550 000 t, about 1/5 of the biomass in the 1960s. By 1978 cod older than 7 yr had declined to about 1/10 of their 1964 level.

Cod Predation on Capelin

Most information on the seasonal feeding behavior of cod was obtained from Hamilton Inlet Bank in central 2J at the time of high cod stock biomass in the early to mid-1960s. During the January–May period when the cod were concentrated in the warm, deep water they were feeding at a low intensity on invertebrates, but as they moved into shallower water and toward shore in early summer they fed intensively on capelin. Predation on capelin remained high in early fall, but became less intense toward December as the cod returned to the warmer slope waters (Templeman 1965; Templeman and May 1965; Turuk 1968). The distinct seasonality in feeding and the presumed importance of capelin in the annual cycle were supported by observation that the cod livers enlarged quickly in summer, remained large through the fall, and declined through winter and spring to a low in May–June (Turuk 1968).

The seasonal feeding pattern in 3K and 3L is basically similar to that in central 2J. A spring–summer period of intense predation by cod on capelin in inshore areas during the capelin spawning season is well-known (Thompson 1943; Templeman 1965). In addition, there is predation on capelin at this time on the northern Grand Bank (Popova 1962; Turuk 1968; Stanek 1975; Minet and Perodou 1978) and on offshore banks in 3K, particularly in areas toward the coast (Popova 1962). However, unlike cod overwintering on the Hamilton Inlet Bank, cod to the south do feed on capelin in the winter, both on offshore banks in southern 2J and 3K (Stanek 1975; Minet and Perodou 1978) and on the north slope of the Grand Bank in 3L (Templeman 1965; Minet and Perodou 1978; Lilly 1981). The extent of this winter feeding on capelin is poorly known.

The length range of cod that prey intensively on adult capelin is ~40–70 cm, the minimum length being 35 cm and the upper length being variable, possibly depending on the abundance and availability of the capelin (Popova 1962; Turuk 1968; Stanek 1975; Lilly 1981). Cod as small as 20 cm prey on juvenile capelin (Powles 1958; Lilly 1981).

Cod are presumed to prey primarily on adult capelin, because the intense predation in inshore waters occurs during the capelin spawning period. However, there are reports of predation on 10- to 12-cm capelin (probably 2-yr-olds) in northern 3L in March (Templeman 1965; Lilly and Fleming 1981) and on offshore banks of 3K and 3L in summer (Popova 1962; Lilly and Fleming 1981). There is also one report of cod feeding on 1-yr-olds (7–10 cm) inshore in 3K in August (Templeman 1948).

Campbell and Winters (1973) estimated that capelin constitute 32% by volume of the annual diet of cod in NAFO Div. 2J3KLNO, and Minet and Perodou (1978) estimated that capelin constitute 28% by weight of the diet in 2J3KL. Both estimates are based on small data sets with inadequate spatial and seasonal sampling.

TABLE 2. Cod landings by the trap and total inshore fishery (NAFO Div. 2J3KL), mature capelin biomass, cod biomass, and temperature, 1972–79.

	Cod landings (kt)		Mature capelin biomass[a] (kt)		Cod biomass[b] (kt)		June–Sept
	Trap	Total inshore	1	2	Ages 4–7	Ages 4–13	TEMPSUM
Year	X_1	X_2	X_3	X_4	X_5	X_6	X_7
1972	32.5	62.1	1679	234	1177	1593	0.92
1973	16.7	41.6	2181	223	900	1304	1.13
1974	15.6	35.2	1978	254	650	1017	0.39
1975	15.7	41.2	1904	362	399	672	0.99
1976	26.5	59.9	2251	526	398	556	1.63
1977	33.8	72.6	3375	342	751	874	1.08
1978	37.4	81.5	3405	218	1006	1185	1.44
1979	25.5	84.6	548	209	1402	1573	1.61

Correlation coefficients

Trap landings

	X_1	X_4	X_5	X_7
X_1	0.46	−0.05	0.40	0.44

Total inshore landings

	X_2	X_4	X_5	X_7
X_2	0.08	−0.15	0.35	0.70

[a]Estimated biomass on January 1. Estimate 1 from Carscadden and Miller (1980), estimate 2 from Carscadden and Winters (1980).

[b]Estimated biomass on January 1, from Wells and Bishop (1980).

Cod Growth

One of the most dynamic characters of cod that might be affected by the change in food supply is growth. However, growth may also be affected by the abundance of the predator, in this case, cod biomass, and by ambient water temperatures. Correlation analyses were conducted to determine if there was any relationship between cod growth and capelin biomass, cod biomass, and water temperature.

To provide annual mean lengths for ages 4–8, length frequencies from the inshore cod trap fishery of Div. 2J3KL, collected in July (mainly) and August, 1970–77, were applied to age–length keys of the inshore fishery. Estimates of growth for each of Div. 2J, 3K, and 3L were calculated by subtracting individual cohort mean lengths from the succeeding year. The values were averaged to provide an index of annual growth for each area and for the Div. 2J3KL stock for 1970–78 (Table 1).

The average growth over the 8-yr series is 6.25 (SE = 0.48) cm/yr. There was no significant difference between mean growth indices of cod from Div. 2J, 3K, and 3L. However, the annual growth indices were not correlated in all cases (Table 1). The growth indices of cod from Div. 2J and 3L were correlated, but the growth index of cod from Div. 3K was significantly different from the indices in both Div. 2J and Div. 3L. Thus, although the mean growth over the period considered was similar in all areas, the pattern of annual growth was different between areas. As a result, cod growth in relation to the other variables was examined using both separate (2J, 3K, 3L) and combined indices (2J3KL).

Because the growth index was indicative of cod growth at ages 4–7, the total cod biomass for these age-groups (Wells and Bishop 1980) was also used (Table 1). Both total and mature capelin biomass from the two series of estimates (Carscadden and Miller 1980; Carscadden and Winters 1980) were used (Table 1). The index of water temperature (TEMPSUM) was derived by summing the monthly mean water temperatures at 25-m intervals, from surface to bottom, from July to June at Station 27 (47°32.5′ N, 52°35.2′ W) near St. John's (Table 1). The July–June period was considered to correspond to the period from which growth indices were derived. Station 27 is the only source of long-term seasonal temperature data in the Atlantic coast area of Newfoundland.

Correlation analysis was conducted using all indices of cod growth and all other indices, singly, in pairs, and all together. None of the relationships was statistically significant ($P < 0.05$) (Table 1).

Inshore Cod Fishery

There is persistent anecdotal evidence that the availability of cod to inshore gears, especially trap nets, is dependent on the appearance of capelin. The obviously heavy feeding on capelin by cod taken in inshore gears suggests that the cod are following the capelin in a feeding migration.

Correlation analysis was conducted relating cod trap catches and total inshore cod landings to mature capelin biomass, cod biomass, and water temperature. Only mature capelin biomass (both indices — Carscadden and Miller 1980;

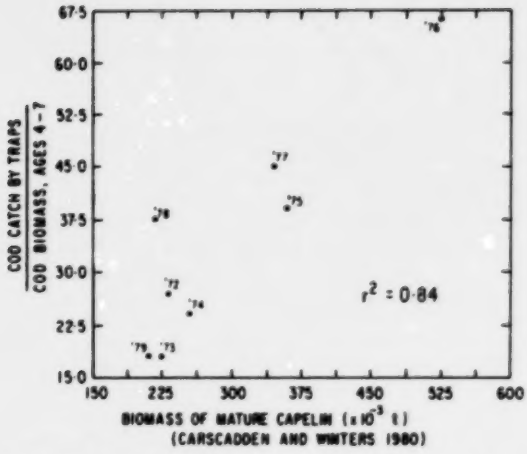

FIG. 3. Relationship between index of availability of cod to the trap fishery and biomass of mature capelin (Carscadden and Winters 1980), 1972–79.

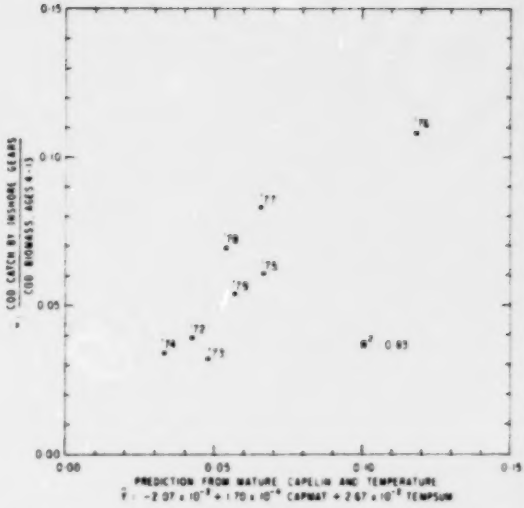

FIG. 4. Comparison of observed index of availability of cod to the inshore fishery and the prediction of that index from a multiple regression on biomass of mature capelin (Carscadden and Winters 1980) and TEMPSUM, 1972–79.

Carscadden and Winters 1980) was used as cod move inshore and feed on capelin during the capelin spawning migration. Cod biomass for ages 4–7 (Table 2) was used to relate cod trap landings because this is the age range usually taken in traps. Cod biomass for ages 4–13 (Table 2) was used when the relationship between cod biomass and total inshore cod landings was examined. The index of water temperature was derived by summing the monthly mean water temperatures at 25-m intervals, surface to bottom, from June to September at Station 27. This period corresponds approximately to the inshore cod fishery.

Trap landings and total inshore landings were regressed against each other and were regressed separately against each of the four variables (Table 2) for the years 1972–79 inclusive. The trap catches were positively correlated with the total inshore catches ($r = 0.83$; $P < 0.02$). Neither trap catches nor total inshore catches were correlated with any of the other four variables. Temperature explained 49% of variance in total inshore catches, just below the level of significance. Multiple regression analyses yielded no significant correlations between trap or total inshore catches and the other variables.

It was postulated that the changing availability of cod to the inshore fishery was a function of the capelin biomass and temperature. The index of availability of cod to the inshore fishery was calculated as follows: (a) trap landings divided by the cod biomass of ages 4–7 and (b) total inshore landings divided by the cod biomass of ages 4–13. On average this fraction was 0.035 for traps and 0.060 for the total inshore fishery. The trap index and one mature capelin biomass index (Carscadden and Winters 1980) were positively correlated ($r = 0.92$) (Fig. 3). There was no significant correlation between trap index and temperature or the other capelin index. There was a significant positive correlation between the total inshore cod fishery index of availability and one mature capelin biomass index (Carscadden and Winters 1980) ($r = 0.81$); the addition of temperature to the regression increased the r to 0.91 (Fig. 4).

Discussion

Numerous studies of the food of cod in NAFO Div. 2J3KL have shown that at certain times and in certain areas cod feed on capelin. Estimates for the Newfoundland area in general suggest that capelin comprise about 30% of the cod's diet. Furthermore, capelin is the major prey of cod taken by the inshore trap fishery. Such information has resulted in the general hypothesis that cod are dependent upon capelin, and that a reduction in capelin stocks, such as might result from a fishery, will have a detrimental effect upon the cod and the inshore cod fishery. Because no studies have been directed specifically at these problems, a correlational approach has been adopted, using annual growth as an indicator of the cod's well-being and inshore catch as an indicator of the intensity of the cod's inshore migration. From this analysis, there was no correlation between cod growth and capelin abundance, cod abundance, and water temperature. However, there was a positive correlation between cod trap availability index and mature capelin biomass as well as between the availability index of the total inshore cod fishery and mature capelin biomass and temperature. Because of uncertainties in the data (discussed below) we suggest that these statistically significant relationships should be taken not as unequivocal proof that such relationships do exist in nature, but that they should be used in determining the direction of future experimental research.

The correlational approach is not ideal; however, the authors felt that uncertainties in all of the data sources precluded a more sophisticated analysis. Differences in the estimates of capelin abundance remain unresolved; annual determinations of cod length-at-age were made during the feeding and growth period rather than at the end; differences

in the indices of growth of cod from different areas could not be resolved; the index of inshore migration is catch rather than some measure of catch per effort; and the mean temperatures at Station 27 may not faithfully reflect the temperature encountered by the cod, especially as they approach the shallow inshore areas. Even if more appropriate data were available and the real relationships are close, it is likely that the estimates of growth, biomass, and extent of inshore migration would contain high observational variance, so that significant correlations could be determined only after many more years of observation than the present 8 (cf. Gulland1965). Furthermore, the available data on cod growth relate to a period of reduced cod abundance. The importance of capelin may become more apparent as the cod stock recuperates.

The present analysis provides no useful evidence for testing the importance of capelin to cod but does suggest areas of concentration of future research. Determination of the contribution of capelin to the cod's diet on an annual basis requires seasonal feeding information from the entire distribution of the cod stock. Because the acquisition of such information for a series of years may be prohibitively expensive, it may be considered sufficient to monitor the cod's somatic and gonadal growth at the end of each year, and to relate this to the abundance of capelin. However, the cod is known for its broad and variable food spectrum. It may therefore be necessary to determine the amount of feeding on other moderate-sized pelagic organisms, including Arctic cod, sand lance, and squid, and to determine the extent to which reduced availability of the larger pelagic prey can be compensated for by predation on shrimp, crabs, and plankton, especially hyperiid amphipods and euphausiids. These benthic and planktonic crustacea comprise a large portion of the cod's diet, and it is possible that their stocks may be sufficiently large to provide adequate forage during a short period of reduced capelin abundance. Without detailed annual information on the cod's food spectrum and the availability of various prey, it may be impossible to interpret any annual differences observed in the cod's growth, reproduction, and mortality.

It is of interest to note that on the Flemish Cap, an isolated bank east of the northern Grand Bank, a separate cod stock exists in the absence of capelin. There are only two abundant species on Flemish Cap, cod and redfish. Changes in the availability of small redfish from recent large redfish year-classes have been tentatively identified as responsible for very large changes in the growth of Flemish Cap cod (Lilly 1980).

A lack of detailed data also hinders examination of the importance of capelin to the inshore cod fishery. Although cod and capelin tend to arrive in inshore waters at about the same time, suggesting that the cod may actively follow the capelin toward shore, there is also anecdotal evidence that either species may arrive inshore unaccompanied by the other, and that the arrival of the cod is also closely related to the warming of inshore waters. Elucidation of these relationships requires a site-specific study of the inshore migration, in which the abundance and movement of both cod and capelin can be related to changes in oceanography.

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Adaptive Management Based on Structure of Fish Assemblages of Northern Continental Shelves[1]

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Difficulties of managing ocean fisheries on a species-by-species basis arise due to catches of mixed species, data requirements for yield models for the large numbers of species within a region, and problems in accounting for species interactions in yield estimates. Furthermore, models have shown that the goal of yield maximization from an assemblage of species with a range of productivity capabilities leads to a reduction in the number of species that supply the yield. Sustained high productivity of those remaining species may not be possible in the simplified system. There is also the risk that return to the original species composition will not result from subsequent reduction of fishing effort. An operational characterization for management purposes is given for an assemblage production unit of fishes. This unit is a group of trophically coupled, resident species. Temporal and geographic characteristics of component species are selected to make it possible to manage the unit as an entity. Two approaches to adaptive management are proposed. In the adaptive procedure, yield or effort is judged by trial and error, and is modified each year by acting on information from the fishery system from the previous year, or years. The management approach is designed with the expectation of unpredictable, continuous, or periodic change. Procedures are described for natural production systems producing sustainable yields and also for systems in continuous fluctuation, producing highly variable yields.

Key words: fish assemblages, fish communities, community structure, adaptive management, multispecies fisheries

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Les difficultés rencontrées dans la gestion des pêches océaniques sur la base d'espèce a espèce sont dues à la capture d'espèces mixtes, aux données requises pour les modèles de rendement d'un grand nombre d'espèces dans une région et, enfin, aux problèmes que posent les interactions entre espèces dans les estimations de rendement. Les modèles ont de plus démontré que l'objectif d'un rendement maximal à retirer d'un assemblage d'espèces à gamme de potentiels de productivité mène à une réduction du nombre des espèces qui contribuent à ce rendement. Dans le système simplifié, une forte productivité soutenue des espèces qui restent peut n'être pas possible. Il y a également le risque qu'une diminution subséquente de l'effort de pêche n'entraine pas un retour à la composition par espece originelle. Nous décrivons des caractéristiques opérationnelles d'une unité de production d'un assemblage de poissons. Cette unité est formée d'un groupe d'espèces résidentes, unies entre elles par des liens trophiques. Les caractéristiques temporelles et géographiques des espèces constituantes sont choisies de manière à rendre possible la gestion de l'unité comme une entité. Nous proposons deux approches d'une gestion adaptive. Selon ce processes adaptif, on juge le rendement ou l'effort par essai et erreur, et on le modifie chaque année à la lumière de l'information fournie par le système de pêche de l'année ou des années antérieures. Cette approche de la gestion est conçue dans l'anticipation d'un changement imprévisible, continu ou périodique. Nous décrivons des méthodes de conception de systèmes de production à rendements soutenus et aussi de systèmes en balancement continu, à rendements très variables.

General Management Goals

Although it may be possible to develop goals of optimum sustainable yield based on maximization models for some of the dominant species of continental shelf groundfish, there appear to be some insurmountable difficulties in managing most of the species from this orientation. There is first a question of quota implementation, and next a question of whether the data can be gathered. Larkin (1977), for example, has pointed out the impracticability of managing the total continental shelf resource on a species-by-species basis. "It would be necessary to regulate ... where, when, and how much of what kind of gear was to be used, and using that gear

[1]Technical Paper No. 5546, Oregon Agricultural Experiment Station.

in some way that harvested each substock of species in proportion to its capacity to sustaina yield. To accomplish this objective would almost certainly require research and management expenditures that were greater than the value of the resources to be harvested." In any region of temperate continental shelf there are often some 20–30 species of fish that one tends to put in a miscellaneous category in terms of landings. None of these fishes on their own are important to the total catch, but in sum they contribute substantially. This situation is typified by the species group of the genus *Sebastes* of the west coast of North America. In a recent series of research cruises off that coast in 1977, 35 species of *Sebastes* were taken. Although clean catches of some midwater species of *Sebastes* are possible, selective quotas are not realistic because fish are often landed as species mixes.

We propose that there should be a second tier of management goals that are outside the yield maximization paradigm. Management concerns must include not only goals related to maximum sustainable yield (MSY) of target species as modified by social concerns to "optimum yield" (OY), but also fish assemblage maintenance goals. We suggest, as have others (Holling 1978), that the paramount goal for renewable resource management is the preservation of management options. MSY oriented management has been shown with models to simplify fishery systems toward species with highest productivity rates (Paulik et al. 1967). The simplification of production systems toward the more productive stocks is likely already in a progressed state in many freshwater systems (Loftus 1976). We have learned from the Laurentian Great Lakes story that combined human and natural pressures exist that will drastically simplify a huge and complex natural production system. There is a clear possibility that the former relative species abundances — the assemblage structure — cannot be restored in the Great Lakes. Even though fishing effort and lamprey predation have been greatly reduced, a series of species interactions may prevent the return of the earlier relative abundances of the lake trout (*Salvelinus namaycush*), burbot (*Lota lota*), and the species complex of deepwater ciscoes (*Coregonus johannae*) (Kerr 1977; Smith 1970). Though the present Great Lakes disarrangement is not entirely due to fishery excess, the lesson of process irreversibility is there to be considered. Analogous, irreversible disarrangements of assemblage structure could also occur over regions of continental shelf. By itself, the OY approach based on maximization models promotes disarrangements and assemblage simplifications. There is no assurance that simplified, high production portions of formerly species-rich assemblages can persist in ocean systems.

Fish Assemblages on Temperate Continental Shelves

Statistical cluster analyses of research trawling surveys have indicated the recurrent nature of geographic fish species associations or assemblages (Day and Pearcy 1968; Knight and Tyler 1973; Gabriel and Tyler 1980). We define assemblages solely on the basis of geographic distribution, and later discuss functional groupings within the assemblages. Most assemblages are associated with specific depth strata — an expected finding because hydrographic values also change with depth. In the northeastern Pacific off the coast of Oregon, there are four to six assemblages over a depth range of 20–500 m seaward from a point of land (Fig. 1). Relative abundance differences among the 15 common species in five assemblages along a transect at 45°20′N indicate an inner shelf assemblage dominated by two species of elasmobranch, big skate (*Raja binoculata*) and the ratfish (*Hydrolagus colliei*), two flatfishes, English sole (*Parophrys vetulus*), Pacific sanddab (*Citharichthys sordidus*), rex sole (*Glyptocephalus zachirus*), and two species of rockfish, Pacific ocean perch (*Sebastes alutus*) and shortspined thornyhead (*Sebastolobus alascanus*), and outer shelf assemblages dominated by another set of flatfish, arrowtooth flounder (*Atheresthes stomias*), Dover sole (*Microstomus pacificus*), and rockfish, rougheye rockfish (*Sebastes aleutianus*) and darkblotched rockfish (*Sebastes crameri*), Pacific ocean perch, and shortspined thornyhead, sablefish (*Anoplopoma fimbria*), and Pacific hake (*Merluccius productus*), and finally two intermediate depth assemblages composed mainly of species overlapping from the outer and inner shelf assemblages plus canary rockfish (*Sebastes pinniger*) (Fig. 2).

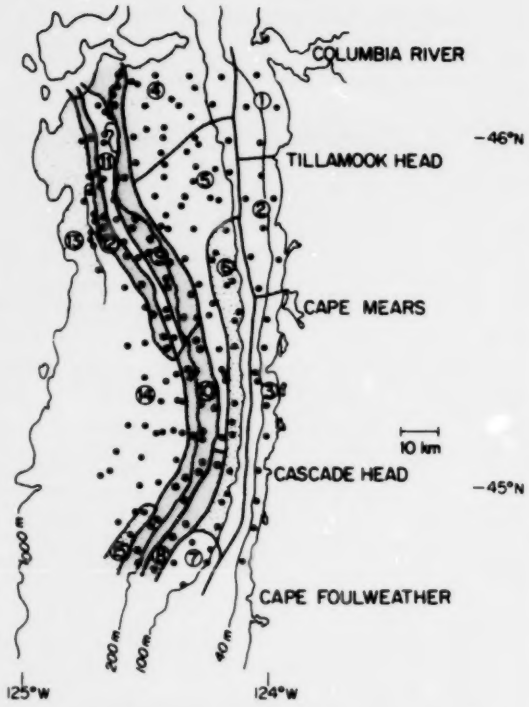

FIG. 1. Areas of the continental shelf off Oregon occupied by summer fish assemblages. Heavy lines are assemblage boundary lines. Finer lines are depth contours. Large dots are trawling sites. Interpreted from Gabriel and Tyler (1980).

The topography of the Scotian Shelf in the northwestern Atlantic is more varied than the shelf off Oregon. The banks and basins strongly affect assemblage distributions. Three assemblages, described in a preliminary study of Canadian research cruises (Knight and Tyler 1973), reflect the topographic structure: the Roseway Basin Assemblage, the Deep

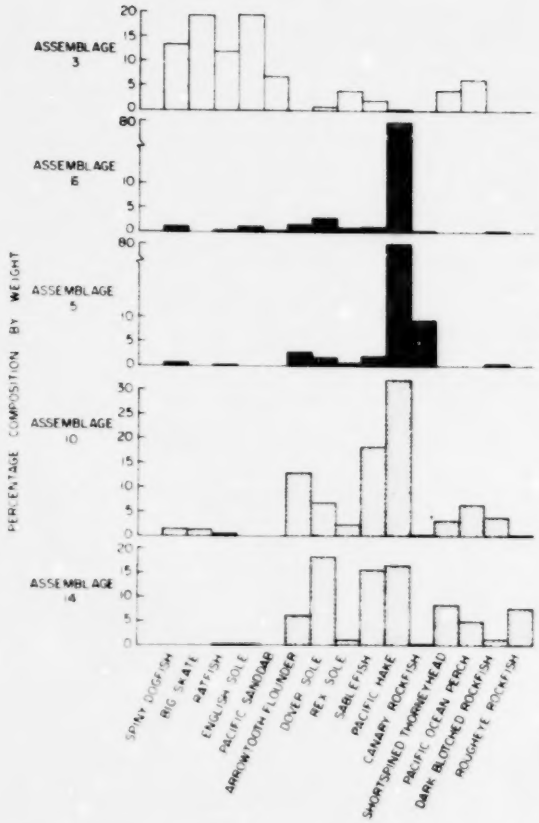

FIG. 2. Percentage species composition of the five summer fish assemblages due west of the point of land on the coast of Oregon at 45°20'N. Lightly stippled bars are from the inner shelf, heavily stippled bars are outer shelf, solid bars are intermediate depths, and represent an overlap between the inner and outer shelf assemblages. Interpreted from Gabriel and Tyler (1980).

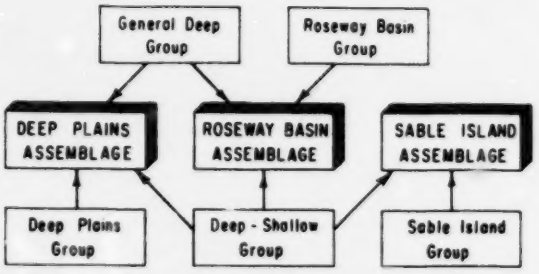

FIG. 3. Spatial groupings of fishes from assemblages of the Scotian Shelf. Some groups are a part of more than one assemblage. From Knight and Tyler (1973).

Plains Assemblage, and the Sable Island Bank Assemblage. These assemblages are made up of species groups that are sometimes specific to a single assemblage, or may be held in

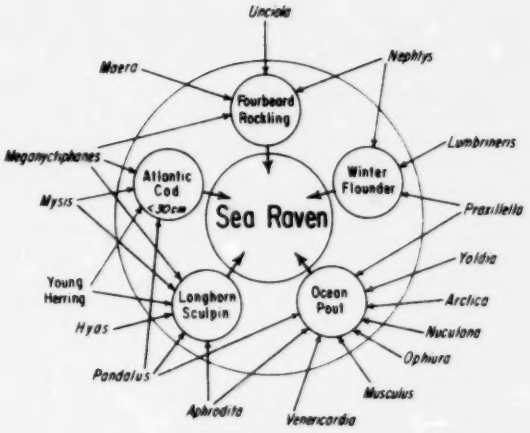

FIG. 4. Energy usage group of the sea raven (*Hemitripterus americanus*), a large piscivorous cottid. Arrows indicate direction of food energy flow. Interpreted from Tyler (1972) and unpublished data.

common by more than one assemblage. For example, the Sable Island Assemblage contains a group held in common by each of the other assemblages (Fig. 3). Similar assemblage structure components have also been found off the coast of Oregon (A. V. Tyler and W. Stephenson unpublished data).

Assemblages of the northwest Atlantic have been described in terms of their temporal components (Tyler 1971). Four assemblages at inner continental shelf locations (Passamaquoddy Bay, Block Island Sound, Long Island Sound, and the mouth of Chesapeake Bay) are comprised of groups of "regulars" (species always present in at least moderate abundance throughout the year), "seasonals" (species at least moderately abundant during either the ocean winter or summer), or "occasionals" (somewhat uncommon species that are found irregularly in trawl samples). Spring and fall did not produce unique seasonal groups, but were transition periods during which summer seasonals were gradually replaced by winter seasonals, and vice versa. The magnitude of the annual change in bottom temperature increased from the northern to the southern locations. This change in annual temperature variation was accompanied by a change in percentage composition of the three components. The percentages of seasonals and occasionals increased with increased annual temperature variation, and the percentage of regulars decreased.

Regulars and seasonals of the assemblage are functionally linked in "food energy usage groups" (Tyler 1974). An energy usage group is the subunit of a foodweb through which energy flows toward a species of particular interest. The usage group is made up of the principal prey of various trophic levels that link up and tend to focus energy towards the selected fish species (Fig. 4). A fishery on the selected species exploits the energy moving through the entire usage group. Of the 35 fishes and principal prey in the combined summer and winter versions of the Passamaquoddy Bay assemblage, 22 species are a part of the energy usage group of the sea raven (*Hemitripterus americanus*), a large, piscivorous cottid (Tyler 1972). There would be several energy usage groups within an assemblage, and they would change in

character by season. Further, some of the usage groups themselves would be linked. For example, the usage group of large, piscivorous Atlantic cod (*Gadus morhua*) would be linked with the sea raven's group because of prey held in common.

An Assemblage Production Unit (APU)

From the foregoing structural characterizations of fish assemblages, we propose a likely multispecies management unit. We suggest that for each fish assemblage that can be delineated from trawl samples there is a geographically limited natural production system of interacting organisms. We consider that those species of the regular group of fishes interacting with one another comprise an "assemblage production unit" (we treat seasonals in the next section). All productivity within this APU is internally, trophically linked.

We mean that two species are trophically linked if (1) food items taken in common are found in the stomachs of at least 10% of the individuals of each species at a moment in time, and in quantities amounting to 10% of an individual's stomach contents, i.e. two species have principal prey in common, and (2) one species is the principal prey of another. We realize that there are other types of species linkages (Tyler 1974) that could be built into our conceptual model, but we opt for simplicity in our conceptual model at this point.

It is likely that there would be more than one APU within a single assemblage region. First, there will not necessarily be functional linkages among all energy usage groups. If there are two unlinked usage groups within an assemblage, then there would be two APUs. Second, APUs in some sense tend to be locally based because they are made up of regulars that do not migrate. Functional linkages and interactions among regular species will be diminished by distance. An assemblage region might be large enough that there would be no interaction between opposite geographic ends. We conceive of the area occupied by an APU as being just small enough that productivity parameters (e.g. species and size-specific growth and fecundity rates) are homogeneous throughout the unit, and that the unit responds in a statistically homogeneous manner to local perturbation of productivity rates. Our concept of statistical homogeneity is the same as that elucidated by Gulland (1969) in his definition of a fishery stock. Gulland distinguishes between a fishery stock and a species population by defining the stock as an operational unit with homogeneous dynamics parameters.

The APU is influenced by, or "driven" by, physical–chemical factors that are forces whose origins are often remote from the geographic region of the APU. For example, coastal upwelling is driven by atmospheric dynamics. The APU also has biotic driving factors operating on it. We conceptualize the seasonal species, and perhaps the occasional species, as driving factors. They invade the area occupied by the APU and must often influence the dynamics of the production processes of the APU, because they may be predators on APU species or else eat the same food items and hence drain off energy that may not always be in surplus supply (Tyler 1972). We prefer to consider the seasonals as driving factors, because to model them we would have to model regions and processes outside of the APU area. In any modeling approach one must set constraints so that the model remains an experimental abstraction of the actual system. The modeler must selectively keep out many of the complexities, using some of them as drivers on the modeled parts.

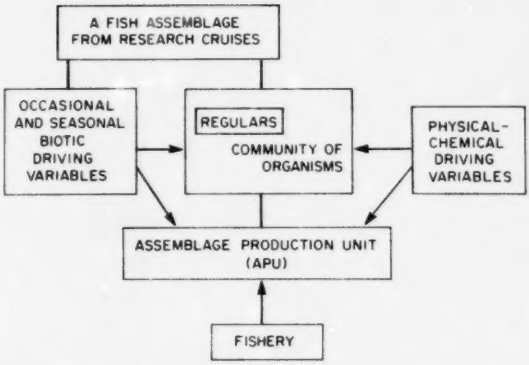

FIG. 5. Schematic placement of an assemblage production unit (APU) in an ecosystem. Arrows indicate influences on the APU. Other connecting lines indicate hierarchial structure.

To summarize the APU concept, the APU is a subset of the regular species, which in turn are a subset of the assemblages determined by research cruises (Fig. 5). The occasionals and seasonals are driving variables or factors operating on the APU. The fishery is also a driving variable operating on the APU.

Emergent Properties

The concept of emergent properties is derived from general systems theory. When we consider a hierarchical organization (e.g. species, community, ecosystem), each level of organization has its own set of definitions, concepts, and principles. Von Bertalanffy (1968) proposes "summative" characteristics and "constitutive" characteristics (emergent properties) for each level: summative characteristics are those which may be obtained by "summing characteristics and behavior of elements known as *in isolation*," whereas constitutive characteristics describe how the elements are linked together producing organization in terms *of a complex*.

Constitutive characteristics cannot be derived from summative characteristics. In other words, emergent properties of a system cannot be discovered by a study of its parts (Dunbar 1980; Kerr 1976). Thus, the characteristics of a complex, compared with those of its elements, appear as "new" or "emergent" (Von Bertalanffy 1968). For example, the principles of programing cannot be derived from the physical laws that govern the operation of a computer at lower levels.

Emergent properties of a system can be obtained *via* any functionally equivalent subsystem: often, elements can be replaced as long as "interactions" remain intact. For example, principles of FORTRAN programing remain the same when applied on an IBM computer or a CDC computer: a do-loop will perform the same operation at the system level, even though the wiring schemes may differ between the two machines at the subsystem level, i.e. the emergent properties are the same though parts have been changed.

The general systems analogy appears to be applicable to

communities, and particularly to assemblage production units. We characterize species populations, as reflected by species composition of an assemblage, as a summative characteristic of our system. We conceive that there could be a cohesiveness within the APU that gives rise to new (emergent) properties of productivity (the constitutive characteristics). We are especially interested in emergent properties that are likely to influence the yields of multispecies fisheries. We postulate that the dynamics variables of uncoupled stock models say little about the yield potential of an APU.

Descriptions of emergent properties of communities have been put forward by other workers (Odum 1969; Holling 1973; ACMRR 1976). We project that the description of emergent properties of assemblage production units will develop as an important aspect of fisheries research. Because fishing effort acts as a perturbation to the system, the emergent properties to be studied for application in fishery management are those related to the behavior of the system in the face of various levels of fishing effort. Some relevant properties are likely to be persistence, stability (sensu Holling 1973), multispecies or APU surplus production (sensu Graham for single fishery stocks), and resilience. We use resilience in the sense of Ricker (1954), but apply the concept to the APU. Resilience is a measure of the rate at which an APU returns toward a dynamic equilibrium level. Other workers have described the resilience properties of the discrete form of the surplus production model formulation (MacArthur and Connell 1966, p. 135–138; Pielou 1977, p. 24–27).

Studying Properties of APUs

In cases where adequate time series exist, community level activity should be described. We should be able to investigate the temporal trajectories of fish assemblage changes with cluster analysis techniques. A null hypothesis, that there are no emergent properties of the assemblage, should be tested. Effects of atmospheric and hydrographic driving variables may be far greater than the effects of species interactions.

We cannot deduce emergent properties by modeling systems with the parts that we happen to know. But mathematical models can provide focus for empirical studies. The two processes of modeling and observation should be used together to investigate multispecies fisheries and to develop management prospectives.

Models may be used to help formulate the interactive mechanisms that give rise to an observed emergent property. These model hypotheses can serve as a basis for empirical investigations to identify critical species interactions. Two possible approaches to the joint modeling–observation process may be used. In some time series, emergent properties such as stability may seem obvious, i.e. recurring structure or recurring structural changes may be observed through many years. We could speculate that the recurring structural changes arise from species interactions, but the number of species interactions might be so large that systematic investigation of them is not possible. We might then turn to homologous, simpler systems in which the same emergent property has been observed. That is, we could adopt a comparative approach of investigation. The interactive mechanisms might be discovered more easily in the simpler system. We might find a repeated association between certain emergent properties and types of species interactions. On the basis of conceptual models synthesized on simpler systems one might construct hypotheses regarding the more complex marine community, and modify data collection procedures to investigate the emergent property and its mechanisms. One could, at the same time, construct computer models to test the relationship between the "simple" system mechanisms and the empirical property that seems to result from them. One problem would be that the model with the "correct" mechanism might not reproduce the real world emergent property (Overton and White 1978).

As another modeling approach, one could start with known emergent properties of a complex marine system, and then try to duplicate these properties with minimum dynamics models based on intuitive conceptions of interactive mechanisms. In this case, emergent properties would have been observed for the complex marine system, but there would be no simpler homolog to garner interactive mechanisms from. Models that reproduced the emergent properties could serve as the basis for planning new field studies that would search for evidence of hypothetical interactive mechanisms.

A difficulty is that more than one system of equations (model) will produce a particular emergent system property. New observations must be made to allow one to discard some of the alternative models. The models themselves will show the nature of the observations required to evaluate hypotheses.

It may be possible to build surplus production models of assemblages analogous to surplus production models of populations. Several studies have already proceeded in this direction. Surplus production as an emergent property of an assemblage is dependent on relative abundance of species (assemblage structure) and also on biomass density (Pope 1976). We propose that it is particularly appropriate to look for this property in an assemblage of interacting species that are regulars within a community, i.e. for an APU. We project that only spurious results will come from attempts to measure surplus production (and other emergent properties) from uncoupled assemblages. To illustrate, if one were to take such an application to its logical but nonsensical end point one would include all groundfishes from all NAFO (formerly ICNAF) statistical areas, and perhaps even work toward a world model.

Adaptive Surplus Production Management

This plan would be developed in two phases that would be instituted sequentially. We consider the set of similar (near-replicate) APUs within an assemblage region as the composite management unit. In keeping with the paramount management aim of maintaining management options, the first phase is to find the highest sustainable effort or catch level that would continue the viability of all species of the set of APUs.

The second phase would be to modify the effort level to provide a sustainable yield-mix (multispecies), and also adequate catch tonnages, consistent with socioeconomic requirements, but that allow APU species to be viable. First we would address the biological problem of determining sustainable yields from similar APUs. When the limits of biological productivity are discernable, we would apply socioeconomic requirements. In the absence of information on how assemblage structure changes at different levels of fishing, we pro-

pose a management plan that will explore a range of constant effort levels simultaneously over the set of equivalent APUs. The theory of exploratory or adaptive management has been discussed by Walters (1981). Constant effort would be arranged among APUs through a range of catch/effort levels from zero to very high. The maximum catch taken from some of the APUs should considerably exceed the MSY for the most productive species, i.e. the low sustainable yields from very high constant effort should be determined. For other APUs, catch should be zero (or no effort). Fishery control could be accomplished either through tonnage quotas, or by varying the time period that the various APU areas are open to fishing. The quotas would be unspecified as to species mix, i.e. the fleet skippers and processors would determine the mix. The mix in the catch would have to be roughly consistent over the APUs, and through time. The APUs that remain continually closed would essentially be fish refuge areas. The refuge areas would mitigate the intentionally high fishing rates on other APUs. After this first phase of constant, multilevel effort is complete, the refuge areas should facilitate the recovery of assemblage structure in areas of heavy, annual effort, through gradual dispersion from the refuges.

The decision to end the first phase of effort application will depend on observed progress in understanding the relationship between multispecies sustainable yield and constant effort. Sustainability, after the usual Schaefer sense of constant annual catch, is multispecies equilibrium catch after fishing-up has occurred (Ricker 1975). This equilibrium would depend on the possibility of dynamic equilibrium for the relative abundance of species, as well as on the equilibrium of absolute species density (Pope 1976). Presumably, the APUs, each with different effort levels expended on them, would reach rough equilibrium levels. Multispecies equilibrium catch would be plotted against effort with the expectation of some sort of dome-shaped curve. We might conceivably see this curve within 5–10 yr of monitoring the several preset levels of fishing effort. Variance due to areal differences in hydrographic variables might have to be accounted for.

However, it is not clear that we will be able to find multispecies equilibrium yields. It is probable that the species assemblages will be in a transition state when the adaptive fishery effort levels are first applied, perhaps due to previous rapid changes in fishing effort. Perturbation, due either to within-species density dependence or to interspecies limit cycles, could induce wide, cyclic-form fluctuations. Also, a growing body of literature indicates that oceanographic trends often dominate fish productivity. Under this collection of influences, equilibrium yield would never be approached.

Adaptive Transition-state Management

We will suppose that rough equilibria do not exist at the system level of fish APUs. Large-scale transition states with respect to species relative abundance may be the only reality for some multispecies fishery systems of the continental shelf. Constant, controlled application of effort would seem to be pointless for such variable systems. The general question that we are asking of the multispecies fishery is how much perturbation the APU will take and still be able to recover its structure. Instead of monitoring variable yields from a range

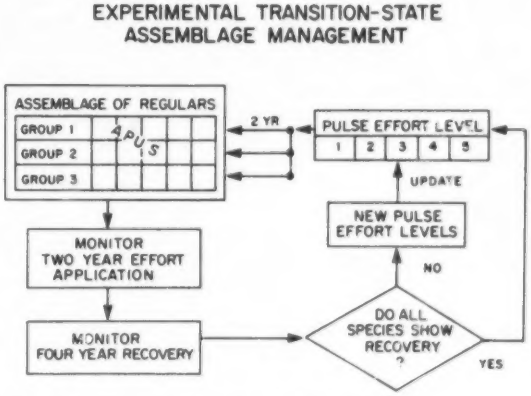

FIG. 6. Schematic of plan for adaptive management of fish assemblage in transition states.

of constant effort levels, one could watch recovery of assemblage structure on roughly equivalent APUs after perturbation by fishing effort pulses of various magnitudes. The pulses would be applied simultaneously to the group of near-replicate APUs with each APU receiving a different effort level. Some APUs would receive zero effort so that a safety effect would be built into the management plan. The first goal of this adaptive program would be to find the limits of repetitive pulse fishing that would allow APU persistence. When this is discovered, the goal would be altered. The second, refined goal would be to find which levels of pulse fishing would produce species catch mixes consistent with socio-economic desires while still satisfying the constraints of the first goal.

We propose a tentative plan for setting up management operation. The specifics of the operation would have to be modified to particular cases. We conceive that the replicate APUs would be divided into three groups, with equal numbers of APUs in each group. Each group would be fished for 2 yr, be unfished for 4 yr, then be fished again, and so on. That is, there would be a 6-yr fishing cycle for each group. At any one time, one group of APUs would be fished and two groups would be unfished except for targetable species deemed not to be part of the APU. Two years after the fishing began on the first group of APUs, it would be shifted to the second group of APUs and 2 yr later to the third group, and so on (Fig. 6). We suggest that 4 yr might be sufficient to observe partial recovery on the basis of observed stock recoveries in the North Sea during World War II. We emphasize that the purpose of the "fallow" period would be to test whether recovery would be possible, i.e. that the system would not shift into a structure dominated by other, undesirable species.

Annual research cruises would be necessary to observe changes in the assemblage structure before, during, and after fishing. We would have to discover which species would be severely reduced in biomass by particular effort levels, and which show no indication of recovery over the ensuing 4-yr fallow period.

After 4 yr of no fishing on the first APU group, fishing would again commence on that group. But those strong effort levels that threatened the viability of some of the APU species

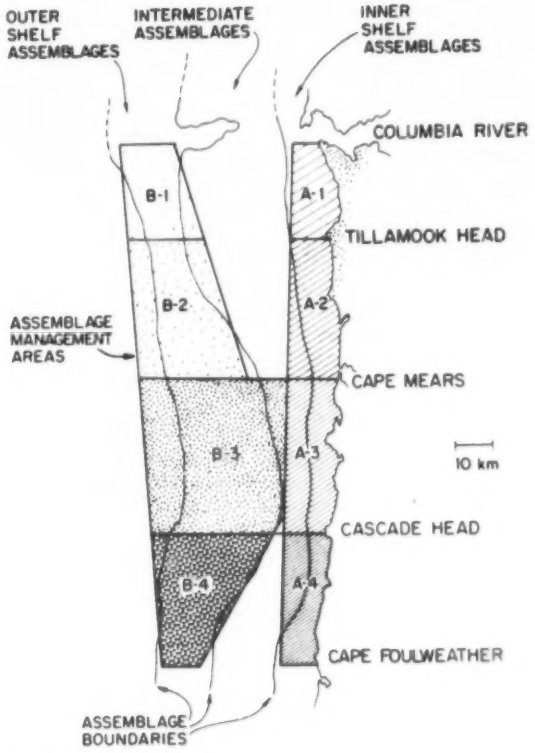

FIG. 7. Arbitrarily mapped assemblage production units, based on assemblage map in Fig. 1. Some of the finer assemblage distinctions were ignored to produce practical management areas.

would be reduced. Light effort levels would be increased toward intermediate levels of effort that did not preclude recovery of APU species.

Concluding Comments on Implementation

What is the minimum preparation necessary to allow an adaptive assemblage program to start? We do not have descriptions of APU structures and distributions. But we suggest that APUs do not have to be mapped accurately to begin assemblage management. Fairly arbitrary divisions within maps of fish assemblages would suffice (Fig. 7). Fishery agencies in many parts of the world already have enough distributional data to map assemblages using cluster analysis techniques. Those maps could be drawn up within a year.

When best-information boundaries are drawn for APUs, information is required to delineate which fishes within the area are functionally linked regulars, because these are the groupings that must be kept track of in an adaptive management program. There are enough data already collected for many continental shelf areas on seasonal translocations of fishes so that regulars may usually be distinguished from seasonals. There are also enough fish stomach analyses in many important fishery regions to construct first approximations of energy usage groups, so that functional linkages within APUs can be proposed. This information could also be put together within a year. Hence, we suggest that after a year's work, management agencies would be in a position to study implementation of adaptive assemblage management. Fairly rapid application need not be stopped by research problems.

Implementation of an adaptive management program will be difficult, because, if for no other reason, there is no explicit tradition of this kind of planning. It would be impractical to bring about the plans suggested here on major fishing grounds during the next few years. One might expect that a demonstration fishery within a marginal fishery area would have some chance of gaining acceptance. Control of effort might have to be effected by time–area closures coupled with an independent means of measuring fishing effort. There might be incentives that could be offered to trawler operators for participating in the fishery on a voluntary basis.

We perceive that many of the traditionally commercial species would lie outside our adaptive assemblage management proposals. Atlantic cod, Pacific whiting, and halibut of both oceans apparently move through several assemblages of regulars, and so do not belong to any one APU. Species with life history stanzas in more than one fish assemblage and species that migrate through many habitats of the continental shelf should be managed on a stock basis, or better, through models of interacting stocks. More selective targeting should be induced on these kinds of species.

The goals of assemblage management proposed here do not involve maximization or optimization. The concern is for maintenance. We propose that assemblages of "miscellaneous" fishes should be kept in such a state that they would be able to return toward their original assemblage structure. Maintenance of miscellaneous species is desirable, either because of evolving management goals, or because the highly productive, more traditionally fished species might not be so productive if the large numbers of miscellaneous species were to become scarce. We emphasize that the reversibility of system simplification is not to be taken for granted.

Acknowledgments

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Bioeconomics of Multispecies Exploitation in Fisheries: Management Implications

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MITCHELL, C. L. 1982. Bioeconomics of multispecies exploitation in fisheries: management implications. p. 157–162. *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59.

Single species management predominates in fisheries management even though in most cases species are interrelated in the ecosystem. This paper examines the inadequacies of the single species approach when applied to multispecies using Canada's east coast fisheries as an example. This is followed by an analysis of the bioeconomic implications of multispecies management with particular reference to competitive and predator–prey relationships.

Key words: fisheries, management, single species, multispecies, bioeconomics.

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Dans les pêches, la gestion sur base d'espèces individuelles prédomine, même si, dans la plupart des cas, il y a interrelations entre espèces d'un écosystème. Nous examinons dans l'article qui suit les défauts de l'approche unispécifique appliquée à des espèces multiples, utilisant les pêches de la côte est du Canada comme exemple. Vient ensuite une analyse des implications bio-économiques d'une gestion multispécifique avec accent sur les relations de compétition et de prédateurs–proies.

Introduction

Fisheries biology and economics, the major disciplines in fisheries management, are dominated by a single species approach to this management. Although in recent years there has been increasing attention to the implications of multispecies exploitation for management by biologists (Muir 1973; Garrod 1973; Ursin 1977), little attention, with few exceptions (Anderson 1977; Huppert 1979; May et al. 1979), has been given to the economic theory of this type of exploitation. One of the main reasons for this is that it has been concluded that the economic analysis of the single species, which has since Gordon (1953) been given serious consideration in the economics literature, applies equally well to the multispecies case. However, a single species theoretic analysis for multispecies can be misleading. As a result, this paper will attempt to pinpoint some of the major theoretical differences between single species and multispecies economic analysis and discuss their implications for fisheries management.

Species Interactions: The Problem Outlined

Most fish species are interrelated in the ecosystem and are exploited on a multispecies basis. This results in two types of interdependence: biological interdependence where a biological relationship links fish stocks, and technological interdependence where different fish stocks are exploited by the same technology (Anderson 1975). For the first, the biological, there are three types of interdependence or interrelationships possible in fisheries and other animal populations: (1) predator–prey, (2) competitively coexistent, and (3) competitively exclusionary (Anderson 1977, p. 113). Of these, it will be shown that (3) is the only case amenable to a single species approach. Despite this the main reasons for the persistence of this approach have been the lack of adequate theories, data, and models, both of an explanatory and predictive nature, for multispecies management. This management is difficult because of the complexity which interrelationships, either biological or technological, impose (Huppert 1979). Some idea of this complexity can be exemplified by Canada's Atlantic coast finfish fisheries although it exists in many of the world's major fisheries (May et al. 1979).

Present Management Problems: Canada's East Coast Fisheries

There is a great variety of finfish resources in Canada's fisheries management areas in the Northwest Atlantic. The major classes, i.e. groundfish and pelagic species, are biologically interdependent in that many pelagic species are the major sources of food (i.e. prey) for groundfish (predators). Both these major classes of fish are technologically independent as they are exploited generally by different fleets, trawlers in the case of groundfish and mainly seiners in the case of pelagics, although there are some vessels, e.g. midwater trawlers, that can exploit both classes. There are also two types of biological dependence between groundfish species where both competitive and predator–prey relationships exist.

The types of interrelationships in Canada's east coast finfish fisheries, ignoring another significant interrelationship due to movement of stocks between inshore and offshore areas, have led to two major management problems which have biological and economic implications. The first, and more important, caused by the predator–prey relationship, is how to manage the exploitation of both groundfish and pelagic species to optimize socioeconomic returns to society. The second and lesser problem, caused by a competitive relationship between groundfish species, is the by-catch problem. This paper will not attempt to solve these problems in Canada's case but to use them to narrow the area of concern to two distinct cases of interrelationship: (1) a

predator–prey interrelationship with technological independence, and (2) a competitive interrelationship with technological interdependence.

This will permit concentration on the theoretical aspects of these two cases and their implications for fisheries management. Before doing so, however, the shortcoming of the single species approach will be outlined.

The Shortcomings of the Single Species Approach

The single species approach to fishery management in both biology and economics is essentially a first step approach and one that is only pertinent in a limited number of cases where stocks are mutually exclusive or independent. In biology the standard single species models, such as the Schaefer logistic or the Gulland–Fox exponential models (Ricker 1975), indicate that growth in landings from man's fishing effort increases to a maximum sustainable yield (MSY) while the underlying population or stock is on the decline (to half its maximum biomass size in the Schaefer and about one-third in the Gulland–Fox models). Exploitation beyond this point leads to lower landings and further declines in the population to the point where extinction takes place, i.e. the inability of the population to recover and sustain itself. These and other models, such as the Beverton–Holt (Ricker 1975), have been responsible for the biological approach to fisheries management of restricting exploitation, mainly through quotas based on MSY or some level below, such as $F_{0.1}$ (ICNAF 1972) in Canada's case.

The single species models have also been responsible for the accepted economic theory of fisheries exploitation (Mitchell 1979). In economics, the main thesis of the economic theory developed since Gordon (1953) contends that under uncontrolled entry, fishery exploitation tends to lead to both biological and economic overfishing. The latter is where the population can remain viable, but can support little or no effort (Anderson 1977, p. 98), i.e. it is not economically worthwhile to exploit. This thesis holds, regardless of whether exploitation is for a single species or multispecies, but there are many interesting differences in the economic implications between these two types of exploitation which will be examined later.

To demonstrate the shortcomings of the single species theoretic approach when applied to multispecies, an examination will be made of how an overall production function of two single species would look from the traditional analysis of Gordon which is static in nature. The shortcomings of this in comparison with more dynamic analysis have been pointed out in the literature (Scott 1954; Clark 1971). However, the static analysis is a good and less complicated starting point to which dynamic elements, if necessary, can be added. Following this approach we shall assume the following: two single species A and B with similar shaped production functions but with differences in resource abundance (fish species, for example, have different growth rates, etc.), that they are exploited by the same units of fishing effort, i.e. technological interdependence, with the same cost per unit of effort, and that the prices of both species are the same and constant, and that zero discount rates prevail.

The economic optima of both species will be given singly, assuming that they are spatially distinct, and then combined

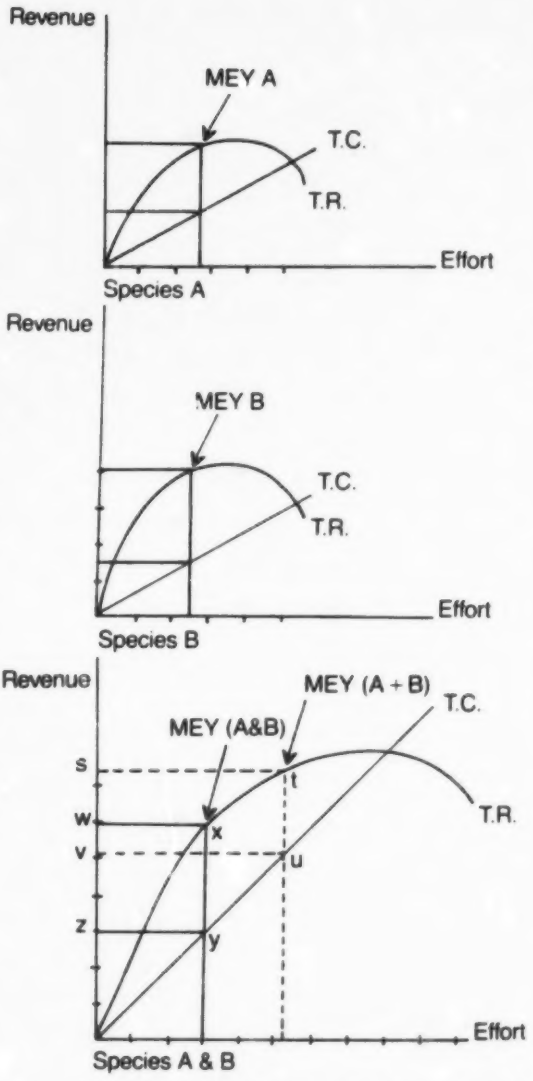

FIG. 1. Single species economic model of two species, separately and collectively. The maximum economic yields (MEYs) of species A and species B are presented; if both species are treated collectively, their MEY is not the sum of their individual MEYs shown by the broken lines. T.C., total cost; T.R., total revenue.

in a multispecies fishery, but in a competitively exclusionary manner (Fig. 1). This figure indicates that the economic optimum level of exploitation, or maximum economic yield (MEY), of both species A and B combined, represented by the area *wxyz*, is not the summation of the economic optimum of A and B, represented by the area *stuv*. The economic optimum, if both species were treated and managed together, is less than the sum of economic optima if they were treated and managed separately. From a purely economic standpoint, the combined management of both species is clearly more

efficient in that the overall rent from the resource is maximized at a lower and less costly level of fishing effort. The figure also indicates how the single species approach can lead to greater overexploitation of resources because, if effort is uncontrolled, the summation of equilibrium economic levels of exploitation in fisheries A and B is also at a much greater level of fishing effort and lower production than if both species were combined.

The foregoing analysis demonstrates that the single species theoretic approach is definitely misleading because the multispecies case cannot be considered merely as the sum of the parts and also because the economic optimum of two species managed collectively is at a lower level of fishing effort than if managed separately.

The Multispecies Case: Biological Considerations

This section will concentrate on two of the three types of interrelationship mentioned earlier: (1) the predator–prey and (2) the competitively coexistent. It will commence first with the biological aspects and will then indicate their economic implications for fisheries management.

Biological Aspects

In predator–prey relationships an increase in growth in the predator stocks means a decrease in growth in the prey stocks which initially might have been responsible for the growth of the former. A decrease in stocks of the prey species, however, results in a decrease in stocks of the predator species. In a competitive coexistent relationship species are intermingled, competing actively for food and space.

Predator–prey relationships have been an important biological concern leading to the development of biological models, such as the Lotka Volterra and others, to explain their impacts on animal population growth. Single species biological models of fisheries population dynamics, such as the Schaefer (1953) model, have also been extended to multispecies through introducing predator–prey or competitive interactions (Smith 1968). The main biological findings from the models have been that growth of animal or fish populations under predator–prey relationships can tend either towards some dynamic equilibrium, and therefore be stabilizing, or can be destablizing by oscillating widely, leading to the extinction of one or other of the species (Clark 1976). Man's fishing effort on an equilibrium predator–prey system can also result in both these states. For the competitive relationship, the abundance of both species is dependent on the amount of food available which would be other fish species, i.e. the prey. One species can predominate in that it might be more adaptable to the environment than the other. There is, however, a competitive equilibrium situation where both species coexist in the environment.

In recent years there have been some complicated theoretical models for multispecies fisheries developed (Andersen and Ursin 1977; Ursin 1977; Laevastu and Favorite 1978); however, few of the models have been used in fisheries management because adequate data for these complex models are difficult to obtain. However, when applied, their findings are interesting. For example, Ursin's multispecies model of the north sea fisheries revealed the following (World Fishing 1979).

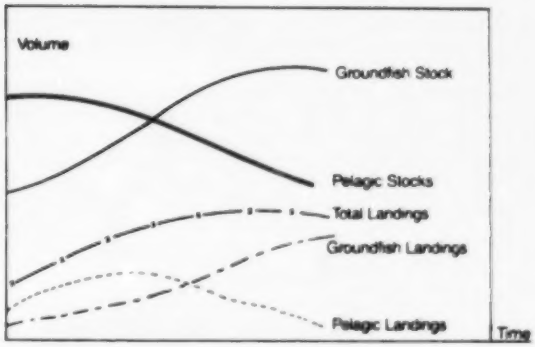

FIG. 2. Stylized version of multispecies model results. The population growth and decline for predator groundfish and prey pelagic stocks are depicted as well as the respective yields for both these groups.

1) There are considerable fluctuations in stock size due to species interactions rather than man's fishing effort. For example, investigations in the Bering Sea indicate that other fish eat 700 000 tons (1 ton = 0.907 184 74 Mg) of herring a year, seals and whales 400 000 tons. Man takes a humble 40 000 tons.

2) The interactions result in increases in some species and declines in others which tend to compensate for each other as overall yields from the fisheries tend to be relatively stable (Fig. 2 is a stylistic version of their findings for major species).

3) Yields and stocks for many species, mainly groundfish, tend to increase together instead of developing in opposite directions as the standard single species biological models indicate.[1]

4) Long-term yields cannot be maximized for each species separately, which breaks down a basic assumption of present fishery regulations.

As a result of these factors, it was concluded that species interactions make decisions on fisheries regulations extremely difficult, and that single species models are completely inadequate when dealing with these problems. The economic and management implications of these findings are important.

The Economic Implications of Multispecies Exploitation

The type of economic problems posed by the exploitation of interrelated species is not new to resource economics as there are similar problems in other renewable or nonrenewable resource exploitation. Numerous models have in fact been developed for these (Solow and Wan 1976; Heal 1976). These models are based on the following factors: (1) resource availability and characteristics, (2) the cost of exploitation, (3) the stock of capital and labor available for fishing effort in fisheries, (4) the demands and prices for products derived

[1]If accurate, this has important ramifications for fisheries population dynamics theory, although there was some support for the standard model in the case of pelagics where the yield and stock developed in opposite directions.

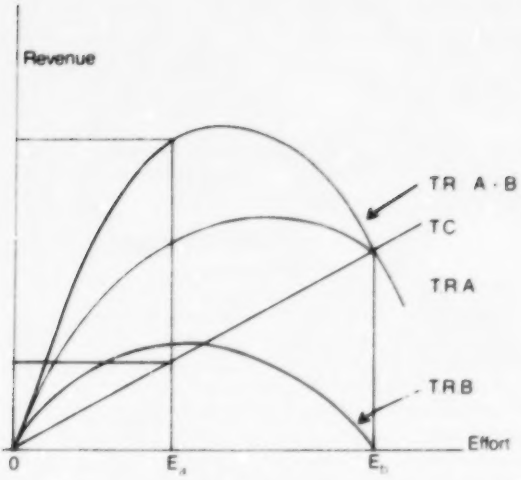

FIG. 3. The by-catch schema. The static economic model of the exploitation of two species which coexist completely and are exploited by the same gear is presented. The model shows the impact that the extinction of one species, the by-catch, can have on the total revenue or production functions.

from the resources, and (5) society's present value of the resources in comparison with their value later on. Sophisticated approaches have been taken to look into these aspects involving control or dynamic optimization theory (Silvert and Smith 1977), but this paper will stick to the more traditional graphical approach as much as possible because it is more familiar to both economists and biologists.

The Competitive Situation: The By-catch Problem

Where a competitive situation exists in which two species are caught by the same gear, problems arise from by-catches in the exploitation of the more abundant species. The traditional approach of single species management is clearly inadequate in this situation because it is generally based on the protection of the less abundant species. As a result, exploitation is usually curtailed for the more abundant, resulting in a dubious biological protection but economic waste (Environment Canada 1976, p. 51).

The by-catch problem can be depicted by Fig. 3. Here two total revenue curves for a dominant species A and competitive but less abundant species B and a cost function for fishing effort are given. This figure shows that, depending on the relative abundance of A and B in relation to the total cost curve, uncontrolled exploitation could lead to the extinction of the less abundant species and the overexploitation of the more abundant species. For example, at the uncontrolled equilibrium level of effort, E_a in the figure, the population of the less abundant species is close to zero and therefore virtually extinct. However, controlled exploitation, based on the economic optimum for both species combined, would probably protect the less abundant species in that the level of effort required (E_a) should not jeopardize the existence of this species. Thus the objective of a combined economic optimum could also certainly have a strong conservation effect.

In some cases, the less abundant species is so small in comparison with the more abundant species that even low levels of fishing effort on the latter would cause extinction of the former. In these cases the less abundant species might have to be written off because the economic gains to society would far exceed the loss of that particular species. This writing off of species is perhaps the most contentious issue between the economic and biological approaches to management. It is, however, a result of single species mangement which aims at protecting virtually every species in the ecosystem. In a multispecies or systems approach, the only level of overexploitation to be feared is that which affects major or dominant species which can then have adverse repercussions on the whole system, i.e. lead to a reduction in total output. If there are species whose loss will not have this effect then their overexploitation should not be problematic.

The relevance of this analysis is diminished by its static nature in real world situations as it is known that one of the by-catch problems is that the less dominant species, being in shorter supply, is usually much more highly priced than the more dominant species. As a result the total revenue curve for the less dominant species would be higher than is shown in the static case (Mitchell 1979, p. 701) and the pressures to overexploit this species correspondingly higher. However, the static analysis is still useful to management. It indicates that in situations where by-catch problems exist it is desirable that the species involved should be treated on a collective basis. For example, if management utilized quota controls, as is the practice in Canada's east coast fisheries, then a combined quota or TAC should be established based on both economic and biological considerations.

The Predator–Prey Situation

Predator–prey situations are more pervasive and more complicated for management than the competitive situation. From the biological growth characteristics, the exploitation of two species (A, the prey, and B, the predator) can result in stable combined yields even if the yields of the predator and prey fluctuate individually (Fig. 2). The experience of commercial fisheries in the North Sea is good evidence of this (May et al. 1979, p. 267). However, it is clear that it is not possible to attain simultaneously MSYs for both species and in fact the biological equilibrium situation is at levels below the MSYs for each species. The type of biological behavior, i.e. stable combined yields with fluctuating individual species yields, is not amenable to the standard graphic treatment in the economics literature and is better handled mathematically (May et al. 1979). However, as pointed out earlier, these are not new problems to economics.

The economic ramifications of predator–prey exploitation stem from the fact that usually both species have to be exploited by different technologies and therefore have different exploitation costs; more importantly, demands and prices, indicating society's valuation of them, also vary. Furthermore, it is not possible to attain maximum economic yields (MEYs) from the exploitation of both species simultaneously. When effort is expanded or contracted for one species there are changes in the revenues and costs of production for both (Anderson 1977, p. 120). It therefore matters whether the predator or the prey is the more important species economi-

cally, and this can be realized by economic factors such as output, demand and prices, number of fishermen or vessels (fishing effort), and estimates of net present values.

The management strategies to be followed, depending on whether the predator or prey species is the more important, will be analyzed assuming high levels of exploitation of both technological independence and effective control over fishing effort. In the case where the predator species B is more valuable to society than the prey species A, then the management objective will be to maximize returns from the exploitation of species B and vice versa if the prey species is more important. This would require, however, two different management strategies. For the first, the maximization of returns from the exploitation of B would require the sustenance of a large population of the prey species A. For the second, this would require a reduction in the predator population B. Thus, for the former fishing effort on A would have to be reduced whereas for the latter fishing effort on B can be increased to attain the desired objectives.

Economic analysis of the two different strategy options can be extremely useful in estimating (a) the economic optimum level of fishing effort for the more valuable species, (b) the economic trade-offs to be made in terms of maximizing returns from one species at the expense (economic loss) of the other, and (c) on the basis of (a) and (b) determining the optimum economic level which maximized the net present value from the exploitation of both species. This type of analysis, by its nature, is dynamic because it is concerned with the rational allocation of resources over time. The net present value obtained by strategies favoring (1) the predator species B and (2) the prey species A would therefore be as follows:

$$(1)\quad \sum_{n=a} \frac{(P_B - L_A)}{(1+r)^n}, \qquad P_B - L_A > 0$$

$$(2)\quad \sum_{n=a} \frac{(P_A - L_B)}{(1+r)^n}, \qquad P_A - L_B > 0$$

where A = prey species; B = predator species; P = profit or rent from exploitation; L = loss from exploitation; r = discount rate; and n = number of years.

In both cases (1) and (2) the profit from exploitation, discounted over time, must be greater than the loss. However, it is interesting to note that the economic loss L would be a minimum or short-term one because exploitation for either species will not take place at uneconomic levels for long. Effort will adjust to levels where total costs equal total revenues, i.e. the equilibrium situation for a free entry fishery. Thus, in the long run L will approach zero.

The analysis indicates that the dynamic equilibrium of predatory–prey exploitation based on the strategies outlined would be where one fishery is economic, generating net present values to society, while the other is operating at levels where net present values are zero, i.e.

$$(3)\quad P = \frac{\text{T.R.} > \text{T.C.}}{(1+r)^n} \text{ and } L = \frac{\text{T.R.} = \text{T.C.}}{(1+r)^n}$$

In the case where the predator is the more important species, it can only attain high levels of output and revenues if there is a trade-off for low output and revenues from the prey. However, if the prey is more important, high levels of output and revenues for both species can be realized. Unfortunately, judging from Canada's finfish fisheries, the latter is not usually the case. These findings, which are consistent with those arrived at by Silvert and Smith (1977) in their more sophisticated mathematical approach, have the most important bioeconomic implications for the multispecies approach to management.

Conclusion

Multispecies management is perhaps the most challenging field in fisheries at this time. Although, because of the complexity due to species interrelationship, a satisfactory management regime has been difficult to implement, the inadequacy of the single species approach indicates that there is little choice but to develop a multispecies management regime. The major requirement for this are (1) biological evidence of the magnitude and extent of the interrelationship between major species, (2) the economic evaluation of the species in question, (3) the establishment of optimum levels of exploitation for society, i.e. making allowances for trade-offs, and (4) the control of fishing effort to attain objectives. Thus, multispecies management will require a more extensive multidisciplinary approach to management than before.

The advantages of a multispecies management regime can be considerable. First, it can simplify management in that it will do away with the necessity for establishing quotas for each individual species. Quotas or TACs would be required for major species or classes in the system. For example, in the case of Canada's east coast fisheries there might be overall quotas for groundfish and for pelagics, with subquotas on the dominant species within them, e.g. cod and herring, respectively. Secondly, this type of regime would require less control on the operations of fishing fleets in that these will no longer be restricted on a species by species basis. Thirdly, they will make these operations more economic by solving or minimizing the by-catch problem and by making trade-offs between the exploitation of predator–prey species which would maximize the net present values from the exploitation of both. These factors are powerful arguments for multispecies management in fisheries because they will result in (1) simplification of management (less regulations) and (2) increasing the possibility for more economically efficient fishing operations.

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Multispecies Interactions Between Fish and Fishermen

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Full utilization of multispecies fisheries requires a management approach that allows for the full complexity of the fishery system and takes into account the social and economic factors that affect the deployment of the fishing fleet. This means in turn that the structure of the fishery should be based on natural functional groupings and not on arbitrary historical divisions. At the most highly aggregated level these are the fish–ecosystem on one hand and the fisherman–processor socioeconomic complex on the other.

Key words: Atlantic cod, capelin, yellowtail flounder, haddock, mathematical model.

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Pour une pleine utilisation des pêches d'espèces multiples, il faut adopter, dans la gestion, une approche qui tienne compte à la fois de la complexité du régime de pêche et des facteurs sociaux et économiques qui influencent le déploiement de la flottille de pêche. Il en découle que la structure de la pêche doit reposer sur des groupements fonctionnels naturels et non sur des divisions historiques artificielles. Au palier de plus haute agrégation, ce sont, d'une part, le complexe poisson–écosystème et, d'autre part, le complexe socio-économique.

The Meaning of Multispecies Management

Multispecies management in any reasonable sense must mean more than the recognition that there exist interactions between fisheries on different species. To identify a set of single species fisheries and then to build a network of interactions between them introduces a vast jump in complexity without providing any way of dealing with the problems of analysis that this complexity engenders. The multispecies approach differs from this in that the existence of interactions between species is recognized at a fundamental level and is followed through at all levels of the management process. The organization of the fishery is viewed as analogous to that of a natural ecosystem, and like an ecosystem it is more easily described in terms of elements having similar function than in terms of species-specific concepts. The trophic-dynamic approach to ecosystem analysis seems appropriate to fishery systems and is the basis for the multispecies models considered in this paper.

As a concrete example, consider a fishery that involves the two species, cod and capelin. The single species view of this system would be to deal separately with a cod fishery and a capelin fishery, taking into account the existence of various types of interaction between them. The multispecies approach would be to recognize a biological subsystem consisting of cod and capelin as well as other interacting species, and a separate subsystem involving the fishermen. One would then focus on the interactions between these two levels of the fishery, namely fish and fishermen, rather than on the connections between two parallel fishery systems.

The advantage of the multispecies approach is that it enables us to take into account interactions of a type difficult to model in single species terms. For example, in the particular model used, it is known that a predator–prey relationship exists between cod and capelin which affects the population dynamics of each stock; this is not difficult to include in the single species approach, as the population dynamics are part of the biological submodel. However, it is also known that capelin affect the cod fishery in other ways, as cod migrate inshore to feed during the capelin spawning season and can be taken by cod traps, but they also gorge themselves to the point where they will not take bait and are not catchable by hook and line; this type of effect is much more easily incorporated in a hierarchically structured model.

The multispecies approach is clearly preferable when one group of fishermen selectively exploits more than one stock of fish. Because the total effort available in the fishery is fixed, a single species type of model requires the inclusion of feedback loops to represent the fact that an increase in the effort directed at one stock must be accompanied by a decrease in effort in the other fisheries; this feedback is implicit in the multispecies model. A situation like this, where components of different single species fisheries are strongly correlated or are identical, can usually be treated more effectively by using a multispecies point of view.

Types of Interactions

Much of the complexity of multispecies management arises from the incredible proliferation of potential interactions that one discovers when more than one species at a time is taken into account. The simplest single species model has only one interaction, that between the fish and the fishermen. If we look at the analogous two species situation we see that instead

of two potential interactions we have six, and for three species we would have 15! It is necessary to recognize which of these play a major role and to incorporate these in our conceptualization of the fishery; another advantage of the multispecies approach is that it often provides a flexible means of recognizing and modeling such interactions.

One can imagine a multispecies fishery in which there are no real interactions, more commonly referred to as a mixed fishery. Models of this type are plausible first approximations to some tropical fisheries, where gear selectivity is often low and hundreds of different species may be represented in a single haul. Although interactions are present, their number and complexity make them impossible to quantify. However, even in the absence of interactions, the presence of more than one species introduces a new dimension to the management problem. Whereas a single stock can be exploited at an optimal level, given a reasonable model of the fishery and clearly specified management objectives, it is not in general possible to achieve an optimal level of exploitation for all species in a mixed fishery (Beverton and Holt 1957). In addition, fishing pressure affects the relative densities of different stocks; one is likely to find that at any compromise level the slower-growing *K*-strategists, which often include the most valuable species, are displaced by smaller and less valuable *r*-strategists, leading to gradual economic decline of the fishery (Pauly 1979).

Many of the important interactions in fisheries occur within a single "trophic level" of the system, such as predator – prey relations between different species of fish or competition between types of fishermen (e.g. gill-netters versus long-liners). As pointed out above, situations in which a group of fishermen divides its effort among more than one species are treated as interactions of this type in single species models but not in multispecies models; the same applies at higher levels of the system, as when a single processing facility is used for several species.

There are also important interactions that connect the levels of a fishery, such as the connection between capelin spawning and the catchability of cod mentioned previously. Distributional effects of this type are common, with predatory fish aggregating about schools of planktivores which are in turn feeding on concentrated patches, and these may be as important in determining catch rates as overall abundance. These distributional effects play a large and as yet incompletely understood role in ecosystem dynamics (Shaw 1978), but without them many fisheries could not exist (Brodie et al. 1978).

We have mentioned only a few of the interactions that may be present in a fishery, and there are also many more levels to the system than just fish and fishermen. Consider, for example, the seal fishery. Here an abiotic factor, namely ice conditions during the breeding season, affects the natural mortality of seal pups directly and also determines their availability to different types of hunting. The seal stocks in turn consume fish, but they also damage nets and serve as vectors for nematode parasites that reduce the market value of otherwise healthy fish; thus seals interact with the cod fishery at at least three levels — they interact with them directly at the biological level, they damage the gear of fishermen, and they affect product value at the processing level.

Modeling Fishermen's Choice

Modeling the dynamics of fishermen is quite different from modeling the dynamics of fish. The most significant difference is undoubtedly the element of choice, in that fishermen can choose where to fish and what gear to use, if indeed they choose to fish at all.

To model fishermen's choice requires that we understand why they fish as they do. One way is to take a purely economic approach and apply the theory of the firm to fishing enterprises. We might, for example, assume that fishermen seek to maximize their profits from the fishery and treat the decision-making process as an optimization problem. The difficulty with this approach is that there are apparently intangible factors, such as risk, comfort, and time at sea, which must also enter into the decision-making process. For this reason a model of fishermen's choice requires a modified approach in which economic theory can provide a basic framework, but in which the parameters of the model must be estimated from observations of the actual behavior of the fishery rather than established on an a priori basis.

A reasonably general submodel of fishermen's choice can be constructed by assuming that fishermen seek to maximize their net benefit from the fishery, where benefit takes into account not only economic considerations but also the above-mentioned intangible factors; this implies that these factors are in principle quantifiable, but we have no direct way of measuring them. The fishermen may choose between various strategies, each of which refers to a decision to use a particular gear in a specific location; the amount of time which a fisherman spends on the jth strategy will be denoted by E_j. The set of all the E_js, which show how a fisherman distributes his total effort, is a vector that characterizes fishermen's choice, and the net benefit from the fishery is some function $B(E_1, E_2, \ldots)$. The problem of modeling fishermen's choice can then be expressed mathematically as the problem of finding a vector of E_js that maximizes the function $B(\ldots)$, with the complication that not all vectors are possible; for example, the total effort $E_1 + E_2 + \ldots$ cannot add up to more than is physically possible, and the allocation of effort is also constrained by restrictions on fishing imposed by management.

One way to arrive at an explicit form for the benefit function $B(\ldots)$ is to assume a set of linear relationships between benefit, effort, and fish yield. This leads to an equation of the form

$$B = \sum_i P_i Y_i - \sum_j C_j E_j$$

where Y_i is the yield of the ith species of fish, and P_i and C_j are, respectively, the unit price received for the ith species and the unit cost of the jth type of effort. Assumption of a linear relationship between yield, effort, and abundance leads to a supplementary equation of the form

$$Y_i = \left(\sum_j q_{ij} E_j\right) N_i$$

where N_i is the abundance of species i and q_{ij} is the catchability of species i for effort j (if effort j is directed at species i,

this corresponds to the usual definition of catchability, but if effort j is directed at another species the value of q_{ij} might better be called the "by-catchability"). Substitution in the preceding equation gives

$$B = \sum_j \left(\sum_i P_i N_i q_{ij} - C_j \right) E_j$$

as the quantity to be maximized, subject to constraints that may exist. For example, limitation on the total effort takes the form

$$\sum_j E_j \leq E^{(\max)}$$

while a TAC (catch plus by-catch) on species i can be expressed as

$$\left(\sum_j q_{ij} E_j \right) N_i \leq (\text{TAC})_i$$

To construct a complete fishery model one needs to couple the submodel of fishermen's choice described above with a biological submodel of the fish populations. One very simple type of model (at least conceptually) is the system of differential equations

$$dN_i/dt = f_i(N_1, N_2, \ldots) - Y_i$$

where $f_i(\ldots)$ is the natural rate of increase (or decrease) of the ith population in the absence of fishing. By coupling these equations to the constrained optimization model of fishermen's choice one has the rudiments of a complete multispecies model of a fishery; it is clear that the form of this model, which corresponds to the hierarchically structured conceptual framework described above, cannot readily be cast in the form of a single species model. In particular, the model predicts that in the absence of constraints to the contrary, effort will be concentrated on those strategies for which $\sum_i P_i N_i q_{ij} - C_j$ is largest, and it is difficult to build this formula for the allocation of effort into a set of single species models.

We now turn to the question of how a model of this type can be used to interpret and quantify "intangible" factors like risk and time at sea as referred to earlier. Imagine that we are dealing with a fishery in which there are no constraints other than one on total effort, which starts with a set of virgin stocks, and which continues long enough for the exploited populations to reach equilibrium. The end result is that all stocks will be fished down to a level such that for all nonzero values of E_j the values of $\sum_i P_i N_i q_{ij} - C_j$ are roughly equal and these values of E_j satisfy the equilibrium conditions

$$Y_i = \left(\sum_j q_{ij} E_j \right) N_i = f_i(N_1, N_2, \ldots)$$

If the values of P_i, N_i, and q_{ij} are known, then the values of C_j for all the strategies for which E_j is nonzero are known to within an additive constant and inequalities can be constructed for the remaining strategies.

As a particular example of this, consider the case of a selective fishery where $q_{ij} = 0$ unless $i = j$, so that the above equations lead to

$$P_i N_i q_{ii} - C_i = P_i Y_i / E_i - C_i$$

being equal for all i. We can therefore infer that the differences in C_i for the various strategies are equal to the differences in the ratios $P_i Y_i / E_i$.

An ingenious test of this kind of model has recently been carried out by Hilborn and Ledbetter (1979) in a study of the British Columbia purse-seine salmon fishery. Instead of dealing with separate species, they deal with populations in each of eight aggregate fishing areas and identify effort in the same way; by definition, the fishery is completely selective. The test is based on the existence of annual changes in salmon abundance, which corresponds in our model formulation to having a different set of $f_i(\ldots)$ each year. The costs of fishing in each area, C_i, which are attributed to risk, travel time, etc., should not vary greatly from year to year; consequently we expect the values of $P_i Y_i / E_i$ to vary from year to year, but the differences $P_i Y_i / E_i - P_j Y_j / E_j$ between pairs of areas should be equal to the differences $C_i - C_j$, and should be constant over time. They find that the data support this prediction, and in a way that implies a reasonable pattern to the costs; the estimated cost of fishing in the exposed waters of the Strait of Juan de Fuca is by far the highest, whereas the sheltered waters of the Gulf of Georgia have the lowest implied cost.

A similar approach is used by Siegel et al. (1979) to compute the harvesting capacity of the New England otter trawl fleet on the assumption that its observed fishing pattern maximizes revenues. However, they attempt to determine the parameters independently of the model and cannot obtain adequate cost data in this way, so their calculations are based on the questionable assumption of maximization of gross revenues.

The use of optimization models for fishermen's choice requires identification of fishing objectives, and the above examples illustrate that these objectives may be quantified either as independent input information (Siegel et al. 1979) or as outputs of the model (Hilborn and Ledbetter 1979). An alternative approach based on statistical identification of a fishery production function has been proposed by Carlson (1975) who shows that for the New England otter trawl fishery it is reasonable to assume that vessels fish to maximize revenues, but that this assumption does not lead to correct predictions for the pelagic Pacific tuna fleet; in the latter case it appears that a principle objective is minimization of time at sea, so that vessels normally harvest less valuable species as encountered rather than continue searching for the more valuable stocks.

Taking a more general approach to the problem of modeling the behavior of fishermen, we can distinguish between two basic methodologies. First, one can study the fishermen and seek through interviews and other socioeconomic research methods to define their goals, which can then be incorporated in a linear-programing or other type of optimization submodel. Some very interesting research of this type has been carried out (e.g. Anderson and Wadel 1972); the need for further work on the needs and objectives of fishermen is recognized (McCracken and Macdonald 1976), but the prospects for reliable modeling of fishermen's behavior on the basis of a reductionist approach are poor. For example, it is

very difficult in this way to allow for changes in the objectives of fishermen that might come about with increases or decreases in net income; such changes represent a type of feedback loop that is very difficult to study in isolation.

A second methodology for the study of fishermen's behavior involves analysis of the entire fishery system to see what kinds of submodels are consistent with the patterns that are observed. This is the process of system identification and represents a "top-down" modeling approach (Silvert 1981, 1982). The studies by Carlson (1975) and by Hilborn and Ledbetter (1979) cited above were actually carried out in this fashion, as in both cases the authors evaluated several different submodels of fishermen's choice and selected the appropriate one on the basis of how well the results fit the observed landings data. This type of trial and error approach to system identification is widely used, although it is inefficient and the modeler may easily overlook good potential models (Kagiwada 1974). Often statistical methods of data analysis can be used to suggest simple but powerful and sometimes counter-intuitive models, and these models are likely to elucidate the feedback structure of the interaction between fish and fishermen more clearly and succinctly than models constructed on "first principles."

Identification of Fishery Systems

The complexity of fishery systems is such that one can seldom estimate in advance how much information and structure is required in a model to simulate the true behavior adequately, or conversely, what type of interactions are implied by observed behavior. For example, there is a well-defined inverse correlation between cod and haddock landings on the Scotian Shelf (Dickie 1965), but the explanation for this could range from a purely biological interaction (e.g. competition leading to correlated changes in abundance) to a purely economic one (shifts in effort in response to market pressures). Effects of this type are generally very difficult to deal with in single species models, but a multispecies approach provides a natural framework for their analysis.

System identification refers to the process of constructing models that behave the same as the system under investigation, and, as the above example shows, such models are not uniquely defined (Kagiwada 1974; Silvert 1981). A common approach to the system identification problem is to construct a set of different models and test them by comparing their outputs with the behavior they are intended to simulate. This is basically the method followed in the above-mentioned work by Hilborn and Ledbetter (1979), Carlson (1975), and Dickie (1965), as well as in Riffenburgh's (1969) paper on the Pacific sardine–anchovy fishery in which he showed that the most plausible reason for the decline of the sardine fishery was biological interactions rather than fishing mortality. In all of these cases the approach was to construct a set of relatively simple speculative models expressing well-defined hypotheses about the dynamics of the system, as opposed to building a single massive simulation model incorporating all of these dynamical effects. This process of finding a minimal plausible model which describes the data rather than building an all-inclusive model which can be fit to the data is the process of top-down modeling described in greater detail elsewhere (Silvert 1981, 1982).

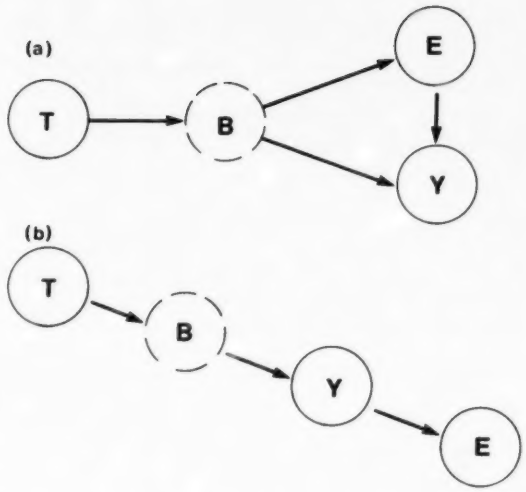

FIG. 1. (a) Postulated relationship between temperature T, biomass B, effort E, and yield Y for the yellowtail flounder fishery; (b) modified relationship, consistent with observed statistical correlations.

Although the trial-and-error approach to system identification is useful, it is a crude method which by its nature is unlikely to lead to counterintuitive results. There are also methods of statistical system identification that can be used to formulate models entirely on the basis of system behavior and may lead to model structures that do not, at least at first, appear to correspond to the expected dynamical features of the system. Both Carlson (1975) and Dickie (1965) used statistical analysis of data to identify a range of possible model formulations, and a statistical analysis of fish catches in the Gulf of Maine by Sutcliffe et al. (1977) indicated that although the variations of individual catches were quite complicated and depended in different ways on a number of external factors, the total fish yield was relatively constant and could thus be modeled in a very simple way (Silvert 1982).

The way in which statistical model identification can lead to counterintuitive results is illustrated by an analysis we have carried out on the southern New England yellowtail flounder fishery. The work of Sutcliffe et al. (1977) indicates that yields of this stock are strongly dependent on lagged sea temperatures, presumably corresponding to changes in survival of the early life stages. Based on these results, we assumed that lagged temperature (obtained from Sissenwine 1974) could be used as a predictor of biomass and we carried out a path analysis (Li 1975) to identify possible causal models relating this independent variable to catch and effort (data from Brown and Hennemuth 1971).

We initially assumed a model structure of the type shown in Fig. 1a, where biomass B and effort E jointly determine the yield Y from the fishery, with a possible pathway from B to E to indicate that effort would probably increase when fish became more abundant. However, the only model that is consistent with the data turns out to be that shown in Fig. 1b, where instead of effort determining catch, catch determines effort! (Temperature predicts 91% of the variance in yield and this in turn explains 88% of the variance in effort. However,

the partial correlation between temperature and effort with yield held constant is only −0.002, so there is no evidence for a direct link between abundance and effort.)

In this case the model, despite its apparent contradiction of the obvious causal connection between effort and catch, is a plausible one; the effort data for this fishery are suspect, and in the next section we show that the way in which commercial catch statistics for this area have been analyzed makes it likely that the effort figures are artifacts of the catch rates. The remarkable feature of this set of fishery statistics is that this conclusion is suggested directly by statistical analysis of the data independently of critical evaluation of the methodology used in gathering them.

Interpretation of Catch Statistics in Multispecies Fisheries

As was pointed out earlier, the distribution of fish and thus their availability to fishermen can be affected by the presence of other species. This is true both of large-scale effects such as the migrations of predators after prey (e.g. cod after capelin or tuna after mackerel) and of local aggregation such as fish schools, the size and behavior of which are known to depend on presence of prey, predators, and other species (Shaw 1978). These effects are complex and as yet poorly understood, but the precise nature of the schooling process can significantly change the catch−effort−abundance relation for the species sought (Clark and Mangel 1979). In terms of a formal model, these distributional effects lead to changes in the catchability matrix, the elements of which describe the availability of fish to different types of fishing strategies.

The presence of other species also affects the allocation of effort by the fishermen. In a totally directed fishery, where it is possible to identify unambiguously each strategy with a single species, one can in principle obtain meaningful catch per unit effort (CPUE) statistics for each species. This ideal situation is rarely encountered in practice, and it is much more common for fishermen to pursue a semidirected strategy of fishing on grounds where several desirable species are likely to be found; the actual process of catching fish may not begin until one of the species sought is encountered in sufficient abundance. In the latter case it is not meaningful to identify effort as being directed at any particular species.

There has been an attempt in some fisheries to assign effort on a post hoc basis by assuming that the composition of the catch must in some way reflect effort directed at a dominant species. The most obvious way of doing this is to assume that the species that is most abundant in the catch was the one at which all the effort was directed, the so-called plurality rule; this was used for assigning effort in the southern New England yellowtail flounder fishery for many years (Lux 1964). Because of the surprising catch−effort relationship which we inferred for this fishery from the path analysis discussed previously, we carried out a simulation of this fishery to see how catch, effort, and CPUE would depend on the relative abundance of yellowtail if effort was assigned by means of the plurality rule.

In our model we assumed that fishermen followed a totally nondirective strategy of searching until a school of fish was encountered and then set a net; we also assumed that all the schools were of the same size and that all species were equally available to the gear. Consequently the composition of the catch at any given time is given by a multivariate Poisson distribution. If the boats stay out until they are full, the distribution of landings is then multinomial. The expected catch of a given species is proportional to its abundance (relative to other species), but the effort as assigned by the plurality rule is a nonlinear function of relative abundance as shown in Fig. 2. When a species becomes scarce it is very unlikely to be the dominant species in a vessel's total catch, and when there are only two species present it is easy to see that the relative CPUE for one of them can never fall below 50% of its maximum value (the higher limiting value of the CPUE curve in Fig. 2 is a consequence of assuming that each load consists of a fixed number of hauls so that the possible distribution of species is discrete — with a more general multispecies simulation the CPUE could fall to a lower limiting value as relative abundance declined, but it would not approach zero).

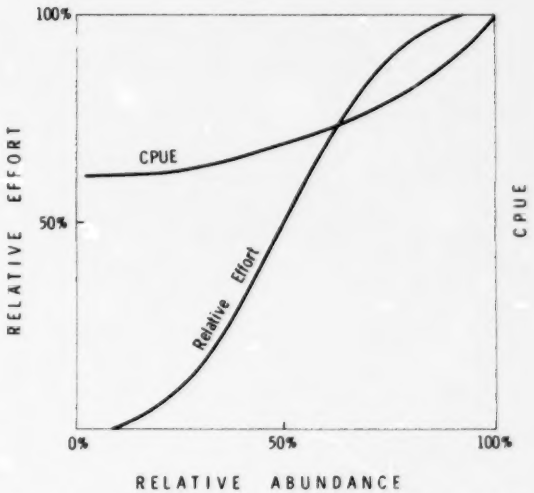

FIG. 2. Relative effort as assigned by the plurality rule and CPUE as functions of relative abundance.

This model shows that the relationship between abundance and effort is quite complicated if effort cannot be uniquely and accurately assigned to a target species. For the yellowtail flounder fishery the simulation supports our empirical conclusion that yield is a better index of abundance than effort, and that effort can be expressed as a function of yield rather than as one of its determinants.

An alternate approach to modeling the catch−effort relationship is to use the general multispecies expression given above to calculate abundance as

$$N_i = Y_i \Big/ \sum_j q_{ij} E_j$$

Although this is theoretically correct so long as the relation between yield and abundance is linear (but see Clark and Mangel 1979), it is unlikely to be of practical value in most cases. It requires determination of the elements of the catchability matrix q_{ij} and accurate identification of the strategies j

and the amount of time E_i spent on each. This is seldom possible, and even if the necessary data are available they are unlikely to be precise enough to give meaningful results.

Because of these problems we feel that attempts to interpret catch and effort statistics in multispecies fisheries along the same lines that have been used for single species approaches will lead to unreliable results. This does not mean that it is not possible to use and analyze these statistics, however. On the contrary, we think that the studies by Dickie (1965), Carlson (1975), Hilborn and Ledbetter (1979), and the path analysis example presented above show that identifiable patterns exist and can be used in the interpretation and modeling of fisheries.

Management of Multispecies Fisheries

Many of the natural implications of a multispecies approach to fisheries management involve considerations that are already recognized in practice. In particular, the trade-offs between different types of fishing activities have usually been taken into account at the political level even though they are rarely included in the formal management policy. When a particular fishery has to be restricted or closed the managers generally can find some other stock to make available to the fishermen. Such compensatory quotas are virtually impossible to deal with in the context of single species models, but they occur regularly in many fully exploited mixed fisheries. Perhaps the best example of a multispecies interaction of this type between stocks having no discernable biological connection is the licensing of offshore lobster boats to compensate the owners for closure of the swordfish fishery in 1971.

One of the most important questions for managers to deal with is whether the policies they implement will have the desired effect. Models of fishermen's choice can play an important role in dealing with this, and frequently the multispecies structure of the fishery has implications that can negate the effect of management regulations. In particular, attempts to regulate the catches in mixed fisheries often lead to suboptimal results because of by-catch effects. In the Scotian Shelf haddock fishery during the mid-1970s it is not clear how effective by-catch restrictions were in reducing the fishing mortality of haddock, but because many haddock were discarded at sea or landed as lower-priced species of fish it is evident that the economic value of the fishery suffered. Because one of the objectives of management is presumably the maximization of financial returns to the fishermen within the constraints imposed by biological factors, it appears that the regulations were to some extent self-defeating.

Many of the factors involved in a multispecies management are under the joint control of government managers and the private sector. A management regime that tries to ensure stable catch levels of each species of fish makes it most profitable to use specialized equipment for each fishery. On the other hand, a multispecies management program that seeks to optimize the fishery by flexible reallocation in response to changes in biological assessments or market demand encourages the acquisition of multipurpose vessels and gear which can easily be switched from one kind of fishing to another. This type of change is already occurring in many fisheries, and there is a pronounced trend evident among both the smaller individually owned vessels and the company-owned trawler fleet. Similar decisions are faced by processors, and many plants are designed with a large number of fairly short processing lines which can easily be switched from one kind of product to another.

Another type of "interaction" which sometimes arises in fisheries management is the "transmutation" of one species to another when the quota has been reached. This is a chronic problem in some fisheries, notably the Scotian Shelf haddock fishery, and it is very likely that appreciable amounts of haddock have been landed as pollock and other groundfish in this region. A similar effect was seen during the period when the swordfish fishery was closed in Canada but open to U.S. fishermen and a number of boats from Nova Scotia would go to sea but would land no fish on their return. Again, these are factors of which the managers are aware, but which have been dealt with as political matters outside the sphere of rational analysis. This reflects in part the fact that such effects simply do not fit into the structure of single species models.

The essence of multispecies management therefore involves more than the formal recognition that there is more than one species of fish in the sea. It means instead the structuring of management about the fundamental natural units of the fishery system, which are the ecosystem on one hand and the socioeconomic framework of the industry on the other. The weakness of single species management is not that it leaves out some effects, but rather that it compartmentalizes the fishery along artificial lines that seldom reflect its actual structure. By using models that more accurately reflect the way in which the entire system operates we can obtain a better understanding of the system and greatly reduce the need to fudge the results of management studies on the grounds of "extraneous factors" or "common sense."

The ultimate step in multispecies management is the restructuring of management itself along the lines described in this paper. There have been trends in this direction during the past few years, notably the implementation of second-tier TACs by ICNAF, but for the most part management operates on a species-by-species basis. In particular, although the decision-making process is structured along the lines of a vertically structured hierarchy, with a group of biologists making a report on recommended fish catches and a separate group of economists reporting on the needs of the industry, the absence of close communication between these groups precludes discussion of the kind of trade-off between different stocks or groups of fishermen that a multispecies approach to management requires. This is not to say that such trade-offs are not made; they are, but generally at the top level of the management structure. This is a workable system so long as all the relevant information can be assimilated and analyzed by a small group of senior managers, but it becomes more and more inefficient as the fishery becomes more complex. As the maritime nations of the world move towards more complete utilization of their fisheries resources the interactions between different components of the fishery will play a larger role in determining optimal management strategy. Unless we develop management methods that can deal with this type of complexity, we may find ourselves saddled with an unstable and unworkable system.

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